Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years

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Abstract. Removal of top-down control on herbivores can result in a trophic cascade where herbivore pressure on plants results in changes in plant communities. These altered plant communities are hypothesized to exert bottom-up control on subsequent herbivory via changes in plant quality or productivity. But it remains untested whether top-down perturbation causes long term changes in plants that ricochet back up the new food chain that depends on them. In a large-scale, 30-yr controlled field experiment, we show that 10 yr of top-down control of an ungulate herbivore (white-tailed deer, *Odocoileus virginianus*) created contrasting forest tree communities exerting bottom-up effects that ricochet back up 3 trophic levels 20–30 yr later. Higher ungulate densities during stand initiation caused significant reductions in tree species diversity, canopy foliage density, canopy insect density, and bird density in young (ca. 30 yr old) forests. Because recruitment of trees from seedlings to the canopy occurs over a relatively brief period (ca. 10 yr), with membership in the canopy lasting an order of magnitude longer, our results show that even short-term perturbations in ungulate density may cause centuries-long disruptions to forest ecosystem structure and function. In documenting this five-step trophic ricochet, we unite key concepts of trophic theory with the extensive literature on effects of ungulate overabundance. As predators decline and ungulate herbivores increase worldwide, similar impacts may result that persist long after herbivore density becomes effectively managed.

Key words: Allegheny hardwood forest; avian communities; canopy foliage; Lepidoptera; *Odocoileus virginianus*; Pennsylvania; trophic cascade; trophic ricochet; ungulate effects; white-tailed deer.

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INTRODUCTION

Dynamics of food chains are shaped by both "top-down" forces like predation and "bottom-up" forces like plant quality and productivity (Hairston et al. 1960, Leibold 1989, Terborgh et al. 2001, Gruner 2004). In the classic top-down trophic cascade, predator reduction increases herbivores, which then attack plants more (Pace et al. 1999). In response, plant density may decrease or plant community composition may shift to dominance by less productive or better-defended (lower quality) species (Leibold 1989, Horsley et al. 2003). These altered plant communities are hypothesized to exert bottom-up control on subsequent herbivory (Feeley and Terborgh 2008) but it remains untested whether top-down perturbation causes long term changes in plants that ricochet back up the new food chain that depends on them.

Across much of eastern North America, the keystone herbivore (Waller and Alverson 1997), white-tailed deer (*Odocoileus virginianus*), has been released from top-down population control

by extirpation of natural predators and inadequate hunting pressure from humans (McShea et al. 1997). Trophic cascades involving deer of various species have been documented in many systems throughout the world following introduction of deer to predator-free areas or following elimination of natural predators (Ripple et al. 2010). Increased herbivory by overabundant deer and other ungulates can delay forest regeneration and change plant species composition (Rooney and Waller 2002, Côte et al. 2004). While delay in forest regeneration is consistent with top-down regulation of plant density, changes in species composition result from herbivore food preference or plant tolerance to herbivory. Hobbs (1996) pointed out that effects of ungulate herbivory immediately following disturbance can, "determine the trajectory of the system among alternative states." We hypothesize that as browse-tolerant trees recruit into the canopy, they exert bottom-up regulation, not on deer, but on canopy herbivores (phytophagous insects) and their predators (passerine birds). Hence, de facto management of deer populations at high density has induced a switch from top-down to bottom-up control of forest ecosystems.

Though several studies have anticipated such shifts (McLaren and Peterson 1994, Terborgh et al. 2001), none we know of has actually followed consequences as they ricochet back up the altered food chain (Fig. 1). Indirect impacts on food chains or other aspects of the ecosystem are not as well studied as direct impacts of deer browsing on vegetation (Rooney and Waller 2002, Côte et al. 2004, Wardle and Bardgett 2004) but these effects are likely to be widespread and pervasive (Rooney and Waller 2002, Ripple et al. 2010). Results from studies on effects of ungulates on insects and their predators have varied and so far few of these has specifically addressed long-term effects of deer-induced changes in vegetation composition (Côte et al. 2004, but see Baines et al. 1994). While negative effects of deer browsing on birds, especially species that utilize ground and shrub layers, are well documented (deCalesta 1994, McShea and Rappole 2000, Stockton et al. 2005), we are aware of no study that has investigated the long-term impacts of browsing-induced changes in vegetation composition on canopy structure or on higher trophic levels in areas established under different known levels of ungulate browsing.

Three studies have experimentally manipulated ungulate browsing across a range of densities to understand effects on ecosystem dynamics: the USDA Forest Service Northern Research Station (Tilghman 1989, deCalesta 1994, Horsley et al. 2003) maintained white-tailed deer across a range of densities for 10 yr (1979–1990) in large enclosures in deciduous forest of Pennsylvania; Tremblay et al. (2007) maintained white-tailed deer for 3 yr (2002–2004) across a similar range of densities during spring through fall in large enclosures, in the boreal forest of Quebec; and Hobbs et al. (1996) manipulated density of elk (*Cervus canadensis*) in sagebrush grasslands of the Rocky Mountains.

These experiments documented thresholds above which ungulate browsing has large effects on dominance patterns of forest tree regeneration (Tilghman 1989, Horsley et al. 2003, Tremblay et al. 2007) or above-ground net primary production (Hobbs et al. 1996).

The Pennsylvania experiment provides a unique opportunity to follow up on how ungulate-induced changes in forest composition of the understory during stand initiation (the first 10 yr following clear cut) shape composition and ecosystem function in the overstory of the regenerated (ca. 30-yr old) closed-canopy forests. We hypothesized that former deer density (1979–1990) would exert lasting, measurable impacts on canopy trees, canopy insects (Lepidoptera larvae), and birds (primarily of the canopy) in the present (2005–2010). Importantly, because deer density was experimentally manipulated and replicated, any significant deer-density effects—direct or indirect—can be inferred to be causal (not merely correlational). Any effects that persist after the 10-yr experimental period represent a biological legacy of past herbivory on the ecosystem.

Methods

Experimental setup

In 1979 and 1980, four experimental sites (two per year) in and around Allegheny National Forest were established by the USDA Forest Service Northern Research Station to study effects of different densities of white-tailed deer on vegetation and birds (Tilghman 1989, deCal-
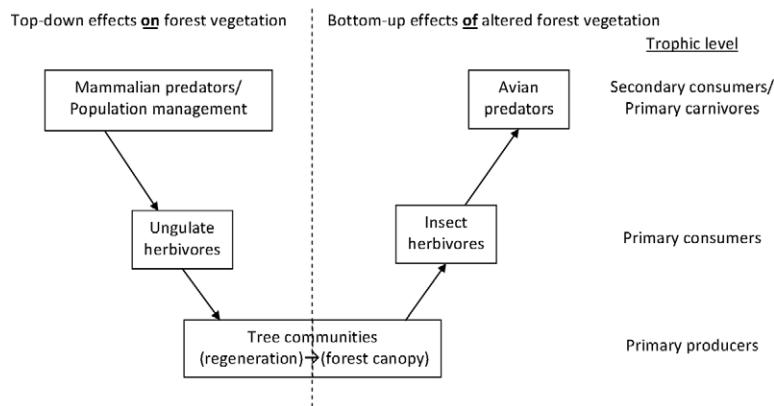
Fig. 1. Conceptual diagram of the trophic ricochet. When mammalian predators of ungulates are reduced, avian predators also are reduced via the trophic ricochet caused by changes in tree community composition. Arrows indicate propagation of effects following perturbation of mammalian predators or population management of ungulate herbivores.

esta 1994, Horsley et al. 2003). Sites represented the range of potential regeneration and site quality conditions for Allegheny hardwood forests, as determined at the start of the study based on amount of advance regeneration present in 1979 (Tilghman 1989). Each of these sites was divided into four experimental enclosures of 12.9 to 25.8 ha wherein were placed 1 to 4 radio-collared deer to achieve deer-density treatments of 3.9, 7.8, 15.6, or 31.2 deer/km^2. Ten percent (1.3 to 2.6 ha) of each enclosure was clear cut to re-initiate stand development. Deer were maintained at these densities for 10 yr (until 1989 or 1990). Due to delays in replacement of deer that died (especially common at high deer density), we report daily average densities for each stand over the 10-yr period. The focus of this study is only on the clear-cut portions of each enclosure because management of other portions after 1990 was inconsistent across study sites or treatments.

Canopy tree density and composition

Three to five permanent 400-m^2 sampling plots were located in each stand (a former clear cut), a ca. 10% sample of the entire stand. Trees were inventoried at 5-yr intervals in each of these clearcut plots to track long-term stand dynamics. All trees >2.5 cm diameter at breast height (dbh) were measured and identified to species. Plots within stands were treated as subsamples for further analysis. Data presented here are from the 2005 census. Deer density effects on forest tree communities were determined using 10-yr average deer density as the independent variable and basal area, total stem density, Shannon diversity (expH, with basal area of each species as the abundance measure, Jost 2006), and percent pin cherry and percent black cherry (the two most abundant tree species; see Table 1 for scientific names of trees) basal area as dependent variables in separate linear regressions using PROC GLM in SAS 9.1. For diversity, percent pin cherry, and percent black cherry, one data point was identified as an outlier and excluded from the analysis. Exclusion of this data point is biologically justified because it was from the site ("Deadman Corners") where it was a priori hypothesized there would be no effect of deer density on forest regeneration.

Canopy foliage density

Foliage provides the basis for most of the canopy food chain and canopy foliage density may provide insectivorous birds with a proximate cue for prey abundance (Marshall and Cooper 2004). We quantified foliage density (leaf area index) using hemispherical canopy photographs taken in June 2009. An average of 18 hemispherical canopy photographs was taken in each stand (262 photos in all). Photographs were obtained systematically throughout the stand at permanently marked understory sampling plot centers. Leaf area index (LAI) was calculated

Table 1. Specific leaf area, leaf area per unit basal area, and basal area (m^2/ha) of dominant tree species in 2005 for experimental clear cuts established in 1979 or 1980 and exposed to different deer densities in northwest Pennsylvania (± 1 SE; n refers to the total number of samples of leaves, number of 400-m^2 plots, and the number of stands in each deer density treatment, respectively from left to right).

Tree species	Specific leaf area ($cm^2\ g^{-1}$) n = 168	Leaf area per unit basal area ($m^2\ m^{-2}$) n = 62	Basal area ($m^2\ ha^{-1}$) across deer density treatments			
			3.9 km^{-2} (3.6–3.9)† n = 4	7.8 km^{-2} (7.8–8.1) n = 4	15.6 km^{-2} (13.5–15.6) n = 4	31.2 km^{-2} (20.9–28.0) n = 4
Pin cherry *Prunus pensylvanica*	278.4 ± 13.8	830.3 ± 130.1	8.40 ± 1.78	10.28 ± 2.04	5.25 ± 1.72	3.93 ± 2.44
Black cherry *Prunus serotina*	315.3 ± 13.0	647.1 ± 53.1	7.20 ± 1.04	6.78 ± 1.73	10.85 ± 1.48	14.55 ± 3.42
Red maple *Acer rubrum*	205.8 ± 13.5	1085.2 ± 296.6	1.40 ± 0.62	1.75 ± 0.74	0.35 ± 0.24	0.28 ± 0.28
American beech *Fagus grandidentata*	301.4 ± 13.5	1253.4 ± 644.9	0.33 ± 0.26	0.40 ± 0.07	0.48 ± 0.34	0.10 ± 0.10
Yellow birch *Betula allegheniensis*	283.0 ± 13.5	1135.6 ± 502.8	0.30 ± 0.24	0.33 ± 0.20	0.40 ± 0.34	0.30 ± 0.21
Sweet birch *Betula lenta*	275.5 ± 13.5	898.9 ± 129.0	4.88 ± 1.79	2.33 ± 1.03	4.30 ± 2.10	0.85 ± 0.78
Other			0.33 ± 0.17	0.50 ± 0.27	0.38 ± 0.19	0.33 ± 0.26
Total basal area ($m^2\ ha^{-1}$)			22.88 ± 0.73	22.35 ± 0.59	22.05 ± 1.24	20.33 ± 1.21

† Target deer density followed by range in actual 10-yr average deer densities in parentheses.

from the central portion of each photograph using Gap Light Analyzer software (Frazer et al. 1999). Samples within each stand were treated as subsamples and were averaged to obtain a single foliage density value for each stand. One of the original stands with target density of 15.6 deer/km^2 was destroyed in 2006 so could not be sampled. Photos from another stand with target density of 8 deer/km^2 were mislabelled and had to be discarded. Effect of 10-yr average deer density on foliage density was analyzed with PROC GLM in SAS 9.1.

Caterpillar density

Caterpillars (larval Lepidoptera) are the dominant canopy herbivores in temperate forests (Franklin et al. 2003). The few studies that have quantified caterpillar density on different tree species have shown tree species can differ 2- to 3-fold in caterpillar density (Holmes and Robinson 1981, Butler 1992, Butler and Strazanac 2000). Insect herbivores commonly specialize on chemically defended hosts by co-evolving metabolic or behavioral mechanisms to avoid or neutralize the defense, but chemical defenses may nevertheless reduce insect growth and fecundity (Price et al. 1980). Hence, chemically defended species like black cherry may have lower insect density than less defended species like pin cherry.

To further investigate whether browsing-induced changes in plant composition ricochet up canopy food chains, in May–June 2009, we sampled caterpillars on branch tips (Leather 2005). Weekly during May, 4 branch tips of all common tree species were obtained from accessible branches in the understory of each stand. In June, sampling was intensified to coincide with peak caterpillar density as reported for nearby areas (Butler 1992, Butler and Strazanac 2000, Marshall and Cooper 2004). To avoid destructive sampling in the experimental sites themselves, we located individuals of the target species adjacent to the experimental sites (see e.g., Butler and Strazanac 2000, Marshall and Cooper 2004). Branches of 5 individual trees of each of the eight most common species in the low canopy (4–10 m above ground) at each of the four sites were clipped using a net and clippers each mounted on extendable poles up to ca. 10 m high (Johnson 2000, Leather 2005). Branch tips (ca. 0.5 m long) were bagged and taken to a central location for processing. Each branch was thoroughly searched for caterpillars. Any caterpillars found were counted, removed and kept for further study and analysis. Branches were dried to constant mass, leaves removed, and weighed. Caterpillar density per kg foliage was calculated for each sample. For analysis, this value was

square-root transformed to stabilize the variance (Neter et al. 1996). Differences in caterpillar density among tree species were determined with mixed models (PROC MIXED) in SAS 9.1 with site as a random effect and tree species as a fixed effect. Following a significant F test (P < 0.05), differences in least squares means were determined among species using LSMEANS.

To investigate legacy effects of deer density during stand initiation on caterpillar density at the stand scale, we scaled estimates of caterpillars per kilogram foliage to estimates of caterpillars per hectare in the regenerated forest. This procedure requires estimates not only of caterpillars per unit leaf mass (c_i for each species i through S, with units kg^{-1}) and estimates of tree density (basal area, ba_i with units m^2 ha^{-1}; methods for both described above), but also estimates of leaf mass per unit basal area of each species (kg m^{-2}; see, e.g., Marshall and Cooper 2004). The relationship between tree size and foliage mass for each species was not available for all species in the study area (specifically pin cherry and sweet birch; Lambert et al. 2005). To obtain these values, in a companion study of 62 400-m^2 plots (forthcoming), we performed multiple linear regression of LAI against basal area of each of the six tree species that collectively account for >98% of the basal area in these forests. Effect of basal area on LAI was significant (P < 0.05) for all species (except American beech with P = 0.0573) and regression coefficients provide estimates of leaf area per unit basal area L (m^2 m^{-2}) of each tree species (Table 1). To convert leaf area to leaf mass, we determined specific leaf area SLA (cm^2 g^{-1}) from leaves collected at the four study sites during early June 2010 (24 samples of each species with 3–6 leaves per sample, depending on leaf size; Table 1). Caterpillar density per hectare C was thus (after applying appropriate unit conversions, e.g., g to kg):

$$C = \sum_{i=1}^{S} c_i ba_i L_i / SLA_i$$

Effect of 10-yr average deer density (1979–1990) on these stand-scale estimates of caterpillar density (2009) were assessed using PROC GLM in SAS 9.1.

Bird density

To assess legacy effects of deer density during stand initiation on birds, we censused birds in each stand (28-yr old clear cut) using 5-minute point counts (Ralph et al. 1993) with each stand censused four times between 31 May and 3 July 2008. One stand with target density of 15.6 deer/km^2 was clear cut in 2006 so was it excluded from bird census. Due to obvious differences in stature of vegetation and small size of the former clear cuts under investigation, edges of stands were clearly discernable so it could be determined with reasonable confidence when birds were actually inside the study stands. All birds detected aurally or visually in the stand were identified to species and tallied. Effect of 10-yr average deer density on total bird abundance (summed across all species and all censuses for each stand) were analyzed using PROC GLM in SAS 9.1. Because stands in the lowest deer density treatment were larger than those in other treatments, we also analyzed trends in abundance for only birds observed within 30 m of the census location. Due to fewer detections in this subset, results were non-significant (P > 0.05), but qualitatively similar to those for all birds within each stand; hence we present results for all birds detected in the stand.

Results and Discussion

By 2005, the initially significant effect (Horsley et al. 2003) of ungulate density on tree density and basal area in experimental clear cuts had disappeared (Fig. 2A). However, tree species composition in these stands remained strongly affected by former deer density: at higher deer densities, stands became increasingly dominated by black cherry (P < 0.0001, n = 15), less dominated by pin cherry (P = 0.0117, n = 15), and lower in tree species diversity (Fig. 2B). Black cherry is more chemically defended than is pin cherry (Burns and Hankala 1990, Eisner and Siegler 2005). This outcome seems consistent with Leibold's (1989) resource edibility theory: plant density is not affected by herbivory (over the long-term) because less palatable (more defended) plants increase to compensate for increased herbivore pressure on palatable species.
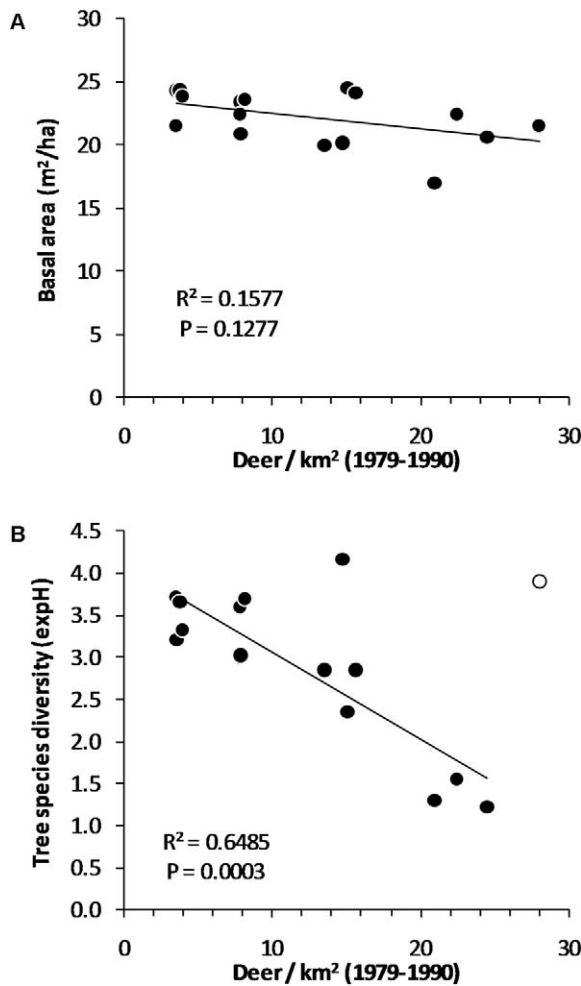
Total foliage density in the canopy in 2009

A

B

Fig. 2. Effect of ungulate density during stand initiation (1979–1990) on forest trees in 2005. Stands were clear cut in 1979–1980. Basal area (A, n = 16) was no longer affected by ungulate density but tree species diversity (B, n = 15) declined significantly with ungulate density. Stem density (trees/ha) was also not affected by ungulate density (P = 0.8934, n = 16). Open symbol in B is an outlier: a high-density stand at a study site where deer density was a priori hypothesized to have little effect on vegetation due to abundant advance regeneration 17. With this stand included, the negative effect of ungulate density on tree species diversity was still significant (P = 0.0361).
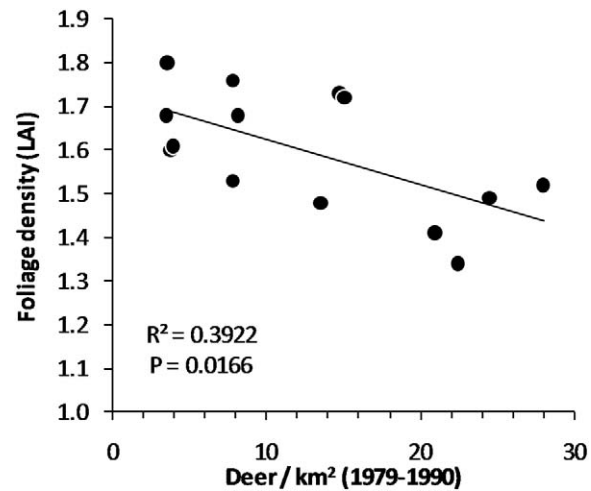

Fig. 3. Effect of ungulate density during stand initiation (1979–1990) on foliage density (leaf area index) in 2009 (n = 14). Data points are stand averages of ca. 18 sample locations per stand.

declined significantly with former deer density (Fig. 3). Percent basal area of black cherry explained 47% of the variance in foliage density across stands (P = 0.0066, n = 14). Foliage biomass per unit basal area differs by tree species (Lambert et al. 2005; see also Table 1). Black cherry (dominant at high deer density) produces particularly sparse crowns compared to most other species in this system (Lambert et al. 2005) and percent basal area of black cherry explained 47% of the variance in foliage density across stands (P = 0.0066, n = 14). Pin cherry (dominant at low deer density) produces soft, porous wood (Burns and Hankala 1990), whereas wood biomass per unit basal area for black cherry is comparable to other species in this system (Lambert et al. 2005). Hence, there is evidence for a shift to higher investment in structural support and chemical defense as herbivore pressure increases, consistent with theory (Leibold 1989). Because interspecific rankings of foliage per unit basal area are largely invariant with changes in tree size (Lambert et al. 2005), the reduction in foliage density caused by higher herbivore density during stand initiation is likely to persist over the century time scale.

In total, 66 caterpillars were captured on 261 branch tips. Tree species significantly (P = 0.0056) differed in mean caterpillar density per unit leaf mass: pin cherry supported over five times the number of caterpillars as black cherry or any other tree species (Fig. 4A). Though the absolute number of caterpillars captured was somewhat small, rankings of caterpillar density on tree
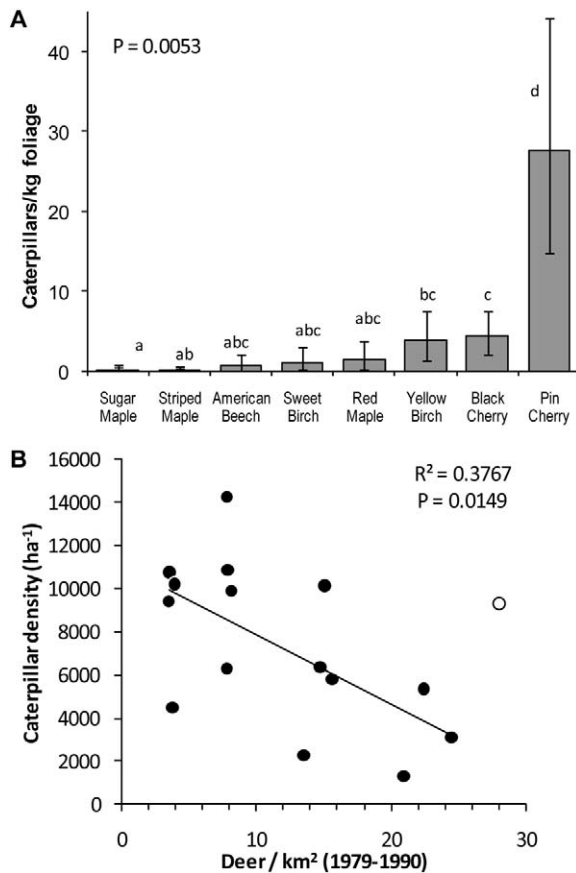
Fig. 4. Effect of ungulate density during stand initiation (1979–1990) on insects in 2005. (A) Effect of tree species on mean caterpillar density per kg foliage (overall P = 0.0056; df = 7, 250). Means of species with like letters do not differ (P < 0.05; means are least square means and bars are ± 1 SE). (B) Caterpillar density per hectare scaled up based on caterpillars per kg leaves (from A), specific leaf area of each species, kg leaves per unit basal area for each species of tree, and basal area of each species of tree in each stand. Open symbol is an outlier (see Fig. 2). Inclusion of outlier made R^2 = 0.1102 and P = 0.2091. Scientific names and basal area of each species in each stand are in Table 1.

species were very similar to those in a much larger sample (660 caterpillars on 968 branch tips) collected from throughout the summer in 2010 (in particular, pin cherry had the most caterpillars, followed by black cherry, as reported here; unpublished data forthcoming). Butler (1992) investigated caterpillar density on tree species in the region and also report higher

caterpillar density on black cherry compared to birches and maples but so far no other study has reported caterpillar density on pin cherry. Hence these results may point to a previously unrecognized value of pin cherry in the forest landscape, namely as habitat for insects and the other species that depend on them.

Our branch-scale results have important stand-scale implications because the tree species most preferred and thus most impacted by ungulates (pin cherry) supported higher densities of phytophagous insects than those avoided by ungulates. This scales up to a significant ungulate legacy effect on insects: caterpillar density per hectare in 2009 declines as former deer density (1979–1990) increases, with a 2.5-fold difference in relative caterpillar density between the highest and lowest deer density, on average (P = 0.0149; Fig. 4B). Even if it were assumed that caterpillar density per unit foliage is constant across tree species, values of foliage density (Fig. 3) provide an estimate of relative caterpillar density that also significantly declines as former deer density increases.

Reduced foliage and caterpillar densities have the potential to reduce density of canopy-dwelling, insectivorous birds (Andersson 1978, Marshall and Cooper 2004). Land use in stands adjacent to the focal stands was highly variable and probably had a large influence on birds within the focal stands. Nevertheless, analysis of 2008 point count data revealed that the legacy of past deer density overwhelmed this noise: the increasing deer density gradient during stand initiation (1979–1990) still caused a decreasing gradient of bird density in these young, closed-canopy forests (Fig. 5, Table 2). DeCalesta (1994) investigated these same stands in 1991 and found a similar trend in avian abundance. Due to the young age of these stands at that time (10–11 yr) this trend was attributed mainly to physical structure of vegetation, specifically reduction in stem density and cover at high deer density. Ungulate effects on birds reported throughout the literature are mainly in species of the shrub and ground layers where ungulate browsing is active (deCalesta 1994, McShea and Rappole 2000, Stockton et al. 2005). In contrast, ca. 30-yr old pole-stage forests investigated here were structurally simple with most vegetation in the canopy (personal observations). Canopy foliage-
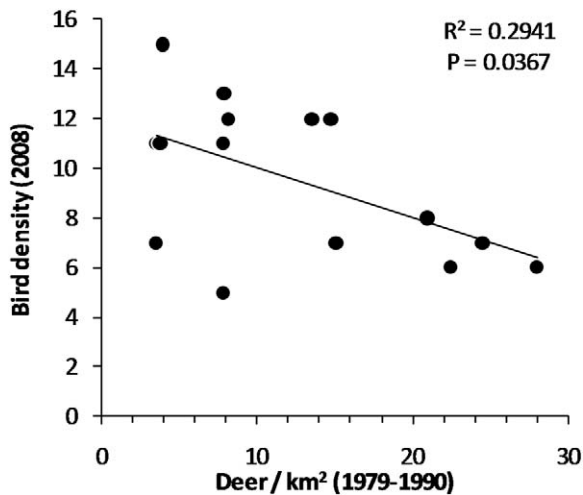
Fig. 5. Effect of ungulate density during stand initiation 1979–1990 on bird density in 2008. Bird density is maximum number of detections across four 5-min point counts inside each stand (n = 15).

gleaning insectivores were by far the most abundant avian guild, comprising 45% of individuals observed (Table 2).

Conclusions

Our study documents a five-step trophic ricochet: top-down release of ungulates has shifted forest tree communities to less-palatable species that present a less dense food resource (foliage) for canopy herbivores (caterpillars) and their predators (insectivorous birds). Furthermore, this browsing legacy persists long after ungulate density has equalized and trees have escaped browsing by growing into the canopy. Though proposed by others (Côte et al. 2004), no other study has provided evidence supporting an indirect trophic (vs. more direct structural) mechanism for a negative effect of ungulate browsing on bird populations. Some authors (e.g., Feeley and Terborgh 2008) infer that when a species of one trophic level (e.g., ungulate) has an effect on species of another trophic level (e.g., insectivorous bird) this constitutes a trophic cascade. However, we draw a distinction: for a trophic cascade per se to operate, the mechanism must be trophic—i.e., through feeding relationships. Ripple and Beschta (2006) documented reductions in several animal taxa likely linked to

deer overbrowsing following predator reduction. Though they termed these effects "cascades", these shifts appeared mediated via physical environmental factors, specifically streambank degradation, not via the food chain. Focusing on below-ground processes, Wardle and Bardgett (2004) reviewed how changes in herbivory by large mammals may also result in a trophic ricochet whereby increased herbivory speeds up nutrient cycling and thereby enhances primary production; however, they did not discuss cascading effects above the primary producer level in the aboveground system.

Though we cannot rule out the possibility that the negative effect of former deer density on total bird density in our study was mediated by some structural aspect unrelated to food availability, our study is unique in providing evidence for two possible trophic mechanisms: foliage density and caterpillar density. Baines et al. (1994) reported that grazing by red deer (*Cervus elaphus*) in Scotland reduced caterpillar density in heathlands by reducing density of plants also preferred by caterpillars and pointed to possible implications for heathland birds. However, ours is the first study to show that ungulate effects on caterpillars mediated by changes in vegetation persist long after ungulate herbivory on those species ceases. To our knowledge, ours is also the only experimental evidence demonstrating negative effects of increasing ungulate density on birds that persist well beyond (decades) the period of experimental manipulation. Indeed, it is the separation in time (ca. 20 yr) and space (understory vs. canopy) of ungulate browsing from their effects on foliage, caterpillars, and birds that allows the trophic mechanism to be separated from the structural mechanism. Over the next decades, differences in caterpillar density per hectare may attenuate as pin cherry senesces (Burns and Hankala 1990) because caterpillar density was relatively similar among the other tree species (Fig. 4A). However, caterpillar density should still decline with increasing former deer density because of the relationship between foliage density and black cherry, which is a persistent member of the forest community. If insectivorous bird populations respond to foliage or caterpillar density (Andersson 1978, Marshall and Cooper 2004), deer density during stand initiation is likely to

Table 2. Mean ($\pm$ 1 SE) number of individuals of each bird species observed in each deer density treatment across four 5-minute point counts conducted June and July 2008 (species are sorted by feeding guild, n refers to the number of stands in each deer density treatment).

Bird species	Feeding guild†	Deer density (deer/km^2)			
		3.9 (3.6–3.9)‡ n = 4	7.8 (7.8–8.1) n = 4	15.6 (13.5–15.1) n = 3	31.2 (20.9–28.0) n = 4
Blue jay *Cyanocitta cristata*	generalist omnivore	0.50 ± 0.29	0.25 ± 0.25	0.33 ± 0.33	
Ruby-throated humming-bird *Archilochus colubris*	hover-gleaning omnivore	0.25 ± 0.25	0.25 ± 0.25		
Ovenbird *Seiurus aurocapillus*	insectivore/molluscivore: ground gleaner	2.00 ± 0.58	1.00 ± 0.41	1.33 ± 0.88	1.00 ± 0.00
Hairy wood-pecker *Picoides villosus*	insectivore: bark gleaner	0.25 ± 0.25			
White-breasted nuthatch *Sitta carolinensis*	insectivore: bark gleaner		0.25 ± 0.25	0.33 ± 0.33	
Black-billed cuckoo *Coccyzus erythrophthalmus*	insectivore: canopy gleaner	0.25 ± 0.25			
Black-burnian warbler *Dendroica fusca*	insectivore: canopy gleaner	0.25 ± 0.25			
Magnolia warbler *Dendroica magnolia*	insectivore: canopy gleaner		0.25 ± 0.25		0.25 ± 0.25
Black-throated green warbler *Dendroica virens*	insectivore: canopy gleaner	1.50 ± 0.29	1.25 ± 0.63	1.67 ± 0.88	0.50 ± 0.29
Scarlet tanager *Piranga olivacea*	insectivore: canopy gleaner	0.25 ± 0.25			
Black-capped chickadee *Poecile atricapilla*	insectivore: canopy gleaner	0.75 ± 0.48	0.50 ± 0.29	1.33 ± 0.88	
Yellow-throated vireo *Vireo flavifrons*	insectivore: canopy gleaner		0.25 ± 0.25		
Red-eyed vireo *Vireo olivaceus*	insectivore: canopy gleaner	2.50 ± 0.50	1.75 ± 0.75	2.33 ± 0.88	1.75 ± 0.25
Blue-headed vireo *Vireo solitarius*	insectivore: canopy gleaner		0.25 ± 0.25		
American redstart *Setophaga ruticilla*	insectivore: canopy sallier		0.25 ± 0.25	0.33 ± 0.33	0.25 ± 0.25
Hermit thrush *Catharus guttatus*	insectivore: ground gleaner		0.25 ± 0.25		0.25 ± 0.25
Northern flicker *Colaptes auratus*	insectivore: ground gleaner			0.33 ± 0.33	0.25 ± 0.25
Black-throated blue warbler *Dendroica caerulescens*	insectivore: understory gleaner	0.25 ± 0.25	0.25 ± 0.25		0.25 ± 0.25
Chestnut-sided warbler *Dendroica pensylvanica*	insectivore: understory gleaner	0.50 ± 0.29	0.25 ± 0.25		
Common yellow-throat *Geothlypis trichas*	insectivore: understory gleaner		0.75 ± 0.25		0.25 ± 0.25
Hooded warbler *Wilsonia citrina*	insectivore: understory gleaner/ sallier			0.33 ± 0.33	
Yellow-bellied sapsucker *Sphyrapicus varius*	omnivore: bark excavator			0.67 ± 0.33	
Cedar waxwing *Bombycilla cedrorum*	omnivore: canopy forager	0.25 ± 0.25	0.25 ± 0.25	0.33 ± 0.33	0.25 ± 0.25
Rose-breasted grosbeak *Pheucticus ludovicianus*	omnivore: canopy forager		0.50 ± 0.29	0.33 ± 0.33	0.50 ± 0.29
Veery *Catharus fuscescens*	omnivore: ground and understory forager	0.75 ± 0.75	0.75 ± 0.48	0.33 ± 0.33	0.25 ± 0.25
Dark-eyed junco *Junco hyemalis*	omnivore: ground forager	0.75 ± 0.48	0.25 ± 0.25		0.50 ± 0.29
Brown-headed cowbird *Molothrus ater*	omnivore: ground forager		0.25 ± 0.25		
Eastern towhee *Pipilio erythrophthalmus*	omnivore: ground forager		0.50 ± 0.29		0.25 ± 0.25
Ruffed grouse *Bonasa umbellus*	omnivore: ground-forager				0.25 ± 0.25

Note: Blank cells indicate zero values.
† Guilds based on DeGraaf et al. (1985).
‡ Target deer density followed by range in actual 10-yr average deer densities in parentheses.

continue to influence avian abundance over the century time scale.

Due to the experimental and long-term nature of our study, our results provide strong evidence that release from top-down control of herbivores can shift ecosystem structure and function to bottom-up forces that ricochet back up the new food chain to primary carnivores. The biological legacy of browsing intensity during the relatively brief period of stand initiation (10 yr) persists for at least two decades after experimental manipulation of ungulate density ended and likely will persist until stand replacement (>100 yr). Deer density at the landscape scale has declined substantially across much of the study area (deCalesta 2009), but the effects of the former experimentally controlled herbivore densities persist in the structure of forest communities, including trees, caterpillars, and birds. Ungulates have thus shifted the fundamental nature of energy regulation in forests over the long-term. Similar mechanisms are likely to pervade other forest ecosystems where ungulate densities are or have been high (see Ripple et al. 2010).

Acknowledgments

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