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Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years

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Summary

1. Ungulate browsers, when at high densities, are major drivers of vegetation change in forests world-wide. Their effects operate via a variety of generalizable mechanisms related to plant palatability and relative growth rate with respect to browsing pressure.

2. Though such impacts are obviously long-lasting when they determine composition of tree regeneration, we document in a unique long-term (30 year) experiment that biological legacies of initial deer density persist in the understorey herbaceous vegetation at least 20 years after deer densities were equalized.

3. We sampled understorey vegetation in former clear-cut areas where density of white-tailed deer (*Odocoileus virginianus*) was manipulated (3.9–31.2 deer km^{-2}) for 10 years (1979–1990), and stands experienced ambient deer density (ca. 10–12 deer km^{-2}) for the next 20 years (1990–2010) to determine whether initial deer density treatments still influenced understorey vegetation in 30-year-old, closed-canopy forests.

4. Stands initially (1979–1990) exposed to higher deer densities had ca. five times higher fern cover and three times the seedling and forb cover in 2010, as well as significantly lower angiosperm species density, compared to stands initially exposed to lower deer densities.

5. These results appear driven by deer avoidance of ferns, allowing them to expand at high deer density and sequester sites for decades.

6. *Synthesis*. Our long-term, experimental results show unequivocally that elevated deer densities cause significant, profound legacy effects on understorey vegetation persisting at least 20 years. Of relevance regionally and globally where high deer densities have created depauperate understoreys, we expect that deer density reduction alone does not guarantee understorey recovery; stands may need to be managed by removing recalcitrant understorey layers (e.g. ferns).

Key-words: biological legacy, determinants of plant community diversity and structure, eastern deciduous forest, ferns, *Odocoileus virginianus*, Pennsylvania, plant–herbivore interactions, white-tailed deer

Introduction

From a variety of studies across the globe, it is now firmly established that high densities of ungulate browsers can dramatically alter not only forest regeneration but also composition, density and diversity of herbaceous understorey vegetation (see e.g. Russell, Zippin & Fowler 2001; Rooney & Waller 2003; Côte *et al.* 2004). These high densities are caused by a combination of extirpation of carnivores, population management by humans, and in some cases introductions (McShea, Underwood & Rappole 1997; Côte *et al.* 2004). Effects of ungulates on trees and herbs appear to be two sides of the same coin: because they browse certain species more than others, high browser densities shift understorey composition away from diverse communities dominated by tree seedlings and wildflowers and towards a few species of unpalatable ferns and shrubs. Hence, ungulate browsers like deer are keystone herbivores (Waller & Alverson 1997) that threaten both forest regeneration and biodiversity of forest vegetation.

But how many deer are too many and how long does their impact persist? Most studies of browser impacts, across

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Europe, Asia, Australasia and North America, have been in the context of natural deer density gradients or exclosure studies with ambient vs. no deer (e.g. Baines, Sage & Baines 1994; Balgooyen & Waller 1995; Coomes *et al.* 2001; Miyashita, Takada & Shimazaki 2004; Stockton *et al.* 2005; Barrett & Stiling 2006; see review by Côte *et al.* 2004). Hence, their results are often contradictory and difficult to generalize. Furthermore, Hester *et al.* (2000) pointed out that because large herbivores are integral parts of many forest ecosystems and their effects are frequently nonlinearly related to their density, studies of herbivore effects must investigate multiple herbivore densities. One study that accomplished just this is the landmark 10-year experiment investigating the effects of white-tailed deer (*Odocoileus virginianus*) in large enclosures ranging in density from 3.9 to 31.2 deer km^{-2} in northern hardwood forests of Pennsylvania, USA (Tilghman 1989; Horsley, Stout & deCalesta 2003). This experiment established that deer densities over ca. 8 deer km^{-2} caused dramatic shifts in vegetation during the stand initiation stage (the first 10 year) compared to lower densities. Specifically, higher densities of deer caused forests to be increasingly dominated by unpalatable tree species and understoreys to be increasingly dominated by ferns and grasses. In a similar, though shorter-duration, experiment in boreal forests of Quebec, Canada, Tremblay, Huot & Potvin (2006) recommended managing deer at densities < 7.5–15 deer km^{-2} for the conservation of browse-sensitive plants. While these studies come to similar conclusions about deer density thresholds, once these thresholds have been crossed, can forest communities recover?

Based in part on guidance from these studies (Tilghman 1989; Horsley, Stout & deCalesta 2003; Tremblay, Huot & Potvin 2006, 2007), in some areas, deer are beginning to be managed at more sustainable levels (see e.g. Royo *et al.* 2010; Tanentzap *et al.* 2011). Nevertheless, decades of deer overabundance have suppressed and locally extirpated populations of many forest herbs; this 'ghost of herbivory past' (Carson *et al.* 2005) may impede their ability to recover. Furthermore, dense cover by ferns and other browse-tolerant species has been shown at least initially to suppress growth and recovery of other species even after deer density was reduced (de la Cretaz & Kelty 2002; Royo & Carson 2006; Tanentzap, Kirby & Goldberg 2012). It is not known how long dense fern layers persist after reduction in landscape-scale deer density and whether recovery of diverse understoreys is suppressed into the long term.

Here, we ask whether the biological legacy of high deer density creates pronounced shifts in the understorey vegetation that persists long after deer density is reduced. Cuddington (2011) defined a biological legacy as 'an indirect effect that persists for a long time period in the absence of the causal species, or after this species has ceased the causal activity'. We investigate long-term effects on vegetation following 10 years of exposure to a range of experimentally manipulated deer densities in the same experimental enclosures studied by Tilghman (1989) and Horsley, Stout & deCalesta (2003). We measured vegetation in 30-year-old forests 20 years after deer density treatments ended, and all stands returned to ambient deer density. We thus generalize Cuddington's definition from the presence or absence of a species, here white-tailed deer, to the gradient of manipulated deer densities and interpret a legacy effect to be present when the former deer density gradient explains a significant portion of the variance in vegetation gradients. Because deer density was controlled along an experimental gradient, our study allows a unique test of deer density legacy effects because inferences on deer density effects do not rely on suppositions about what the 'pre-deer' community was like, a limitation of exclosure studies (e.g. Carson *et al.* 2005) or natural experiments with imprecise deer density estimates (e.g. Balgooyen & Waller 1995). We document strong and pervasive legacies of former deer density on multiple aspects of understorey vegetation in the longest duration-controlled experiment ever undertaken to investigate deer density effects on forest communities. Legacy effects such as these are likely to be general to forests worldwide where similar mechanisms operate.

Materials and methods

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 forest regeneration (Tilghman 1989; Horsley, Stout & deCalesta 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 the amount of advance regeneration present in 1979 (Tilghman 1989). Each of these sites was divided into four experimental enclosures of 12.9–25.8 ha wherein were placed 1–4 radiocollared deer to achieve deer density treatments of 3.9, 7.8, 15.6 or 31.2 deer km^{-2}. Assignment of deer density to each enclosure was randomized. Ten percentage (1.3–2.6 ha) of each enclosure was clear-cut to re-initiate stand development, 30% was thinned and 60% was left uncut; the distribution of these disturbance treatments was designed to mimic disturbance distributions across the Allegheny hardwoods region (Fig. 1; Tilghman 1989; Horsley, Stout & deCalesta 2003). The focus of this study is only on the clear-cut portions of each enclosure because management of thinned and uncut areas after 1990 was inconsistent across study sites or deer density treatments. Within each clear-cut, 3–5 ca 20-m^2 exclosures were established (in 1979–1980) in an initial attempt to investigate effects of zero deer. This aspect of the study was abandoned because it was determined that fences were not high enough to keep deer completely out; however, fence posts and dilapidated fencing were still evident around most exclosures in 2010 and based on dramatic differences in vegetation inside and outside exclosures within high deer density enclosures, it is obvious exclosures were at least partially effective (personal observation). Hence, results presented here may reflect the fact that a small proportion of each stand was exposed to greatly reduced deer browsing, regardless of the deer density treatment assigned to the stand; however, the total area of such exclosures was small and akin to natural refugia that might exist on boulders or tip up mounds (Carson *et al.* 2005; Krueger & Peterson 2006).

Deer were maintained at or near target densities for 10 years (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-year period. Fences were removed in

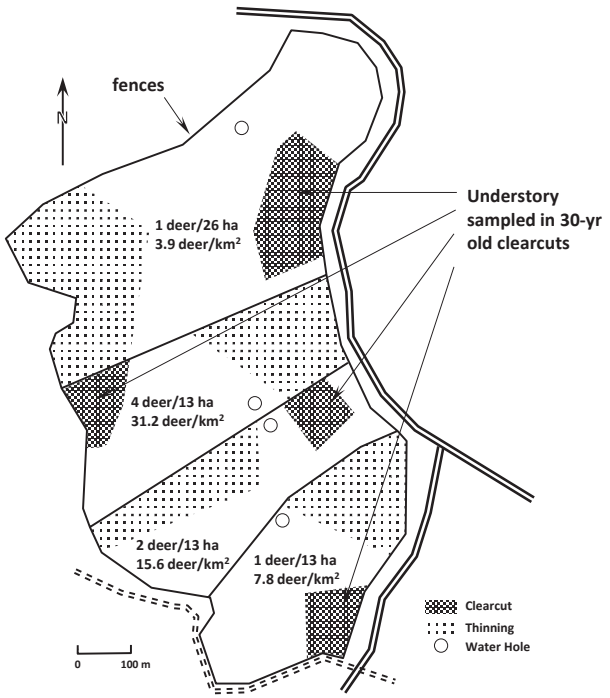

Fig. 1. Map showing experimental design at Fools Creek, one of four experimental sites in north-western Pennsylvania. Deer were held at relatively constant densities inside experimental enclosures at four such sites from 1979/1980 to 1990. In 1990, all fences were removed and sites experienced ambient deer densities of ca. 10–12 deer km^{-2}. In summer 2010, we measured understorey vegetation inside the portions of each enclosure that had been clear-cut in 1979/1980.

1990, and all areas were exposed to regional ambient deer density (10–12 deer km^{-2}, Royo *et al.* 2010) until 2007. One entire study site (Fool's Creek) was refenced from 2007 to 2011 to exclude deer in preparation for timber harvest, while the other three study areas remained unfenced and experienced ambient deer density. One of the original clear-cuts (15.6 deer km^{-2} at State Gameland 30) could not be accessed during this study; hence, we resampled 15 of the original 16 experimental clear-cuts.

Three to five permanent 400-m^2 sampling plots (63 plots total) were located in each stand (each stand originated from a clear-cut), a ca. 10% sample of the entire stand. Overstorey trees were inventoried in 2005 in each of these plots, and analysis of these data is presented in Nuttle *et al.* (2011). Plots were revisited in summer 2010 to sample the understorey. At the four corners of each plot, we estimated understorey composition in 1-m^2 quadrats for vegetation < 1 m tall. Percentage cover of ferns, forbs, graminoids, *Rubus* spp., seedlings and saplings, and unvegetated ground surface (leaf litter) were visually estimated. Ferns were primarily hay-scented fern (*Dennstaedtia punctilobula*) and New York fern (*Thelypteris noveboracensis*), though the category also includes other fern species as well as clubmosses (division Lycophyta). Quadrats within each plot were treated as subsamples for analysis and averaged for analysis of percentage cover data. Additionally, distinct morphospecies were enumerated and pooled for the four quadrats per plot to estimate plant species richness (number of species per 4 m^2; though technically species density, we use the term richness to avoid confusion with individual plant or deer densities). Because we expected ferns to respond differently than other plant species to deer density, we calculated total plant species richness, fern species richness and angiosperm species richness (there were no gymnosperms).

Deer density effects on vegetation were determined using 10-year average deer density as the independent variable and vegetation variables as dependent variables in separate linear mixed model regressions. Percentage cover values in each understorey cover class were arcsine squareroot-transformed for the analysis to stabilize the variance. Residuals of species counts were approximately normally distributed and required no transformation. We performed all analyses in PROC MIXED in SAS 9.3, treating sites as random effects (blocks; RANDOM statement in PROC MIXED) and plots within stands as repeated measures in space (Cardinal *et al.* 2012; here, using the REPEATED statement in PROC MIXED, Moser 2004). This repeated measures design assumes a non-negative correlation between pairs of observations within a stand (Littell, Pendergast & Natarajan 2004) but does not affect the degrees of freedom beyond what is accounted for by site-level blocking (Littell, Pendergast & Natarajan 2004; Moser 2004; Littell *et al.* 2006). While treatments (deer density) were applied to the stand, not to the plot, the distance between plots (> 20 m) far exceeds the interaction distance of herbaceous plants and seedlings within plots (cover of individual plants was generally $\ll$0.1 m^2); therefore, plots could be considered functionally independent of each other (though possibly autocorrelated, as noted above). Others may prefer a more conservative handling of degrees of freedom, which would tend to raise the P values herein presented. So readers may use their own judgment in assessing treatment effects, we present figures showing all data points. Because PROC MIXED does not compute R^2 values, we calculated R^2 as the proportional reduction in variance between random intercept and fixed effects models.

Results

Twenty years after deer density treatments ended (2010), as deer density increases across the gradient of densities maintained during stand initiation (1979–1990), forest understoreys became increasingly dominated by ferns with lower angiosperm richness compared to the more varied understoreys of stands exposed to lower deer density. understoreys of stands exposed to lower deer densities were more patchy and open, with higher woody seedling and forb cover. A number of significant legacy effects of former deer density were evident in the data. There remained a significant, positive relationship between former deer density and percentage fern cover (P = 0.0001, R^2 = 0.1864, d.f. = 1, 58 for all regressions) and a significant negative relationships between former deer density and percentage seedling/sapling cover (P = 0.0013, R^2 = 0.1562), percentage forb cover (P = 0.0010, R^2 = 0.1505) and percentage leaf litter cover (P < 0.0001, R^2 = 0.2219; Fig. 2). There was also a significant positive relationship between former deer density and percentage *Rubus* cover (P = 0.0465, R^2 = 0.0162), but this positive relationship was entirely driven by one site, Fools Creek, which had been refenced to exclude deer for the previous 3 years; when this site was removed, the relationship was no longer significant (P = 0.3223, R^2 < 0.0001). *Rubus* cover was substantially lower, on average, across the other sites (Fig. 2), and though not significant, the relationship between deer density and *Rubus* cover without Fools Creek is weakly negative (Fig. 2). Response of other variables was not dependent on inclusion or exclusion of Fools Creek (Fig. 2). Ferns

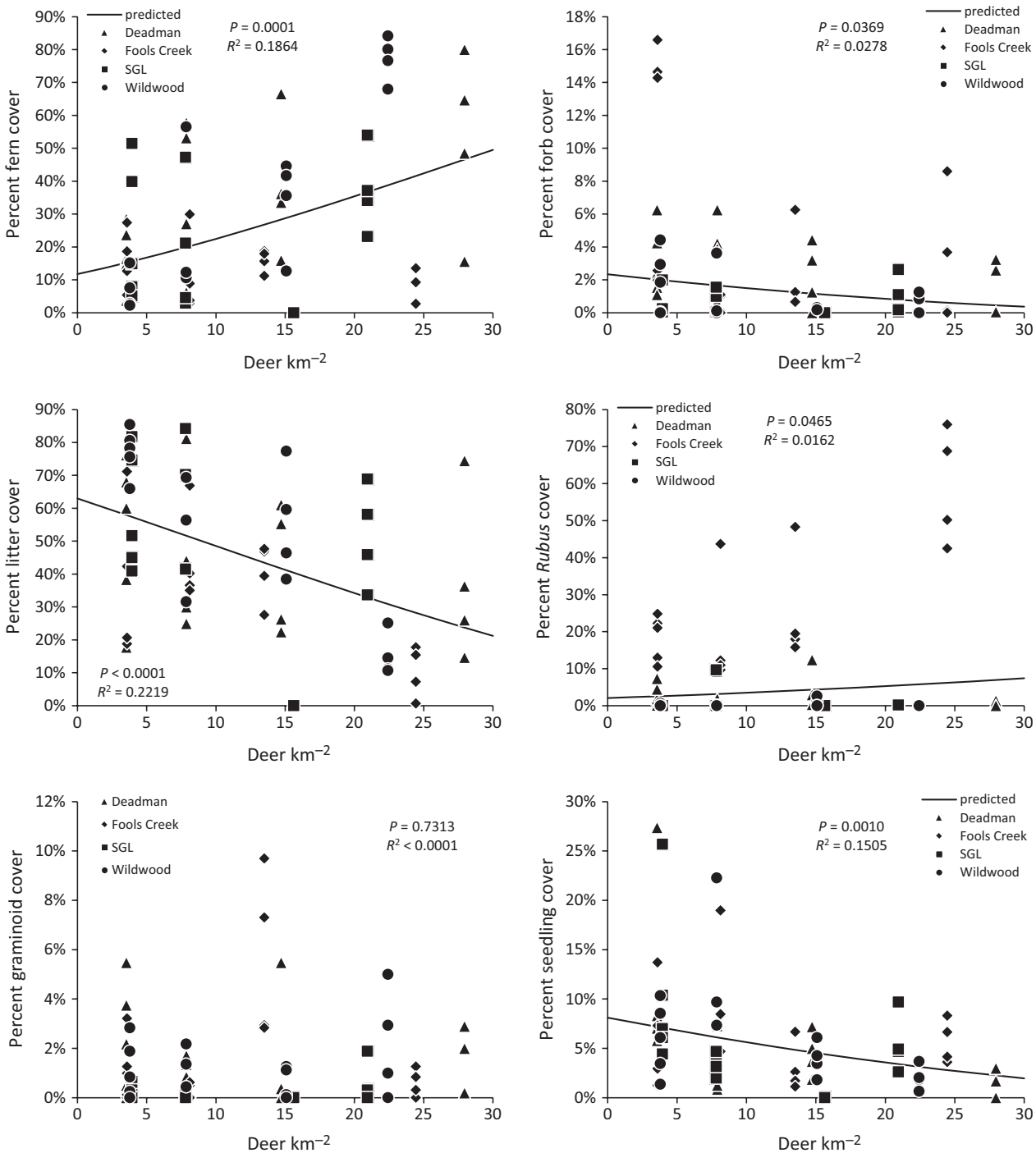

Fig. 2. Effect of deer density during stand initiation (1979–1990) on understorey vegetation cover in 30 year-old experimental stands (2010). Because of occasional deer deaths over the course of the study, stands were not always exposed to the target densities depicted in Fig. 1; therefore, 10-year average deer densities are shown on the *x* axis; stands experienced ambient deer density of ca. 10–12 deer km^{-2} since 1990. Test statistics (P and R^2) are from general linear mixed models (see text), and fitted lines are plotted for response variables with site (block) effects removed for display in two dimensions. Only regressions with significant ($P < 0.05$) slopes are displayed. Study sites are Deadman Corners (Warren County), Fools Creek (Forest County), State Gameland 30 (SGL; McKean County) and Wildwood Tower (Elk County).

and leaf litter (unvegetated ground) were by far the largest contributors to total cover and were significantly negatively correlated ($P < 0.0001$, Pearson $r = -0.54682$). There was no significant relationship between former deer density and mean percentage graminoid cover ($P = 0.7313$, $R^2 < 0.0001$) and graminoids were never more than 10% (typically < 2.0%) of total cover.

Though total species richness shows an apparent week negative trend with increasing former deer density, this effect was not significant ($P = 0.5146$, $R^2 < 0.0001$; Fig. 3). Fern

richness was also not significantly related to former deer density ($P = 0.2850$, $R^2 < 0.0001$) but angiosperm richness was significantly negatively related to former deer density ($P = 0.0365$, $R^2 = 0.0357$; Fig. 3).

Discussion

These long-term, experimental results show unequivocally that exposure to different deer densities during stand initiation causes significant and profound legacy effects on understorey vegetation that persist at least 20 years. Specifically, higher deer densities caused increased fern domination of the understorey, decreased seedlings and forb cover and diminished angiosperm richness. These results largely parallel those reported by Horsley, Stout & deCalesta (2003) during the stand initiation period (1979–1990) and other studies reporting deer effects on vegetation (citations in Introduction). However, our reinvestigation of these long-term experimental plots provides new evidence that initial effects persist through the stem exclusion stage even after deer densities were equalized decades earlier.

For the past 20 years, all stands have experienced roughly equivalent deer densities across the landscape of ca. 10–12 deer km^{-2} (Royo *et al.* 2010; data on file at Warren Forest Sciences Laboratory). This represents a dramatic reduction in deer density for the stands that had been treated with the higher deer densities (ca. 15–30 deer km^{-2}) and a two- to threefold increase for stands that had been treated with the lowest deer densities (ca. 4 deer km^{-2}). Nevertheless, the effects of the initial, experimental deer densities persist despite these dramatic and opposing relative changes. Hence, our carefully controlled experimental results support those of Balgooyen & Waller's (1995) natural experiment of lacustrine islands wherein historic deer density (> 30 year previous) was a better predictor of understorey condition than more recent deer densities. While we hesitate to refer to these divergent conditions as alternative stable states (Beisner, Haydon & Cuddington 2003), due to the successional nature of stands we studied, the simultaneous perturbations of clear-cutting and differing deer densities appear to have set these communities on alternative successional trajectories in both the overstorey (Horsley, Stout & deCalesta 2003; Nuttle *et al.* 2011) and understorey (data presented here).

Dense layers of ferns in the understorey created by high deer densities compete with the wide diversity of plants that may otherwise establish and which prevailed before deer were at high densities regionally (Lutz 1930; Rooney & Dress 1997) and which currently persist in natural refugia (Carson *et al.* 2005). They also create a barrier to tree regeneration which forest managers may go to considerable effort to control (Horsley & Marquis 1983; de la Cretaz & Kelty 2002; Engelman & Nyland 2006). Deer density during the first 10 years of stand development thus appears critical not only to initiating a new stand of trees (something foresters have known for decades), but also over the long term.

Royo *et al.* (2010) investigated understorey vegetation in northern hardwood forests in Pennsylvania, and de la Cretaz

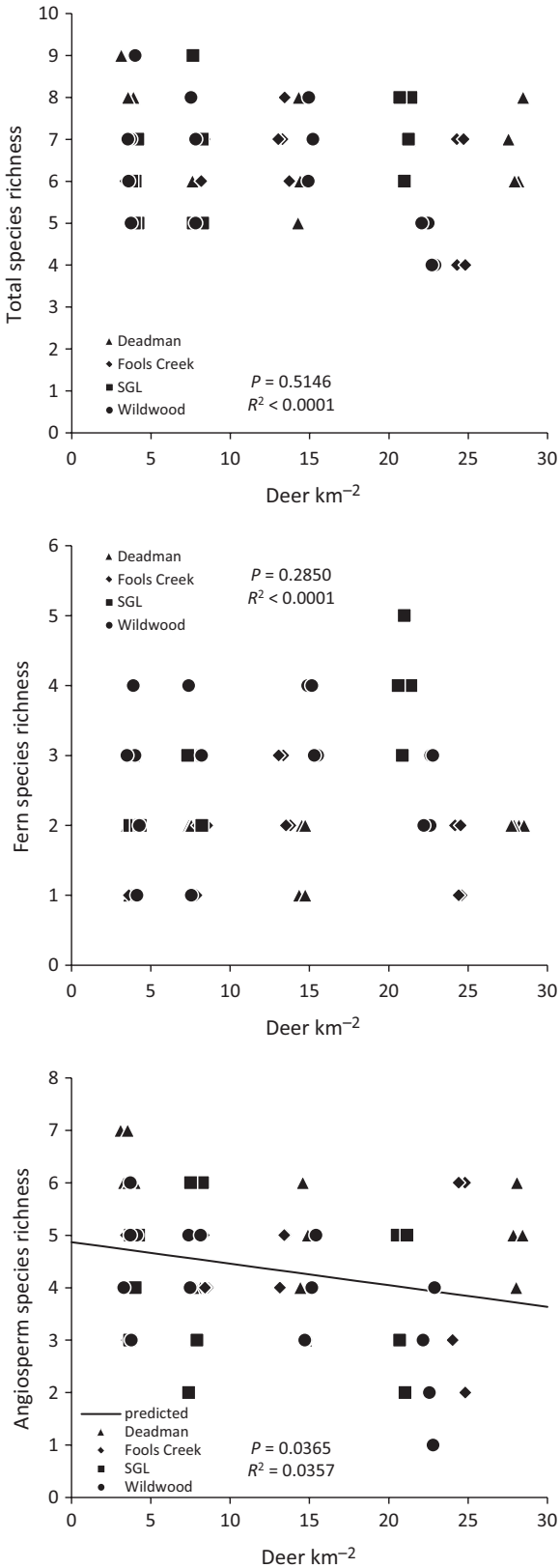

Fig. 3. Effect of deer density during stand initiation (1979–1990) on number of understorey species per 4 m^2 in 30-year-old experimental stands (2010). For display only, values on the *x* axis were jittered ± 0.05 units to reduce overlap in symbols; analysis used the raw values. See Fig. 2 for explanation of *x* axes, symbols and fitted regression line.

& Kelty (2002) investigated tree regeneration in mixed pine forests in Massachusetts, each 3 year after deer population culls had been implemented at the landscape scale following long-term (> 80 year) exposure to high deer density. Both of these studies reported limited recovery of the understorey vegetation but deer legacy effects persisted in the form of dense understoreys dominated by ferns (mostly hay-scented fern). In contrast to those relatively short-term (3 year) results, results presented here show that fern, seedling and forb cover retained legacies of former deer density over the long term (> 20 year) even though all stands had been exposed to moderate deer density for two decades. In these same stands during stand initiation, Horsley, Stout & deCalesta (2003) reported that higher deer densities shifted understorey dominance from seedlings and saplings to graminoids and ferns. Now, those seedlings and saplings comprise the overstorey, and light levels are too low across all treatments to support graminoids or much else except ferns (Hill & Silander 2001; even during the 10-year stand initiation stage, graminoids declined over time as ferns became established; Horsley, Stout & deCalesta 2003). Additionally, quantification of deer effects on understorey vegetation using exclosure studies is often confounded by the possibility that local species pools are reduced, impeding ability of sites to recover even in the absence of deer browsing (Carson *et al.* 2005). Despite low plant density and high variability, there was enough signal in the data to show a significant legacy effect of former deer density in that plots exposed to the lowest deer densities still had ca. three times higher forb and seedling cover and about twice the non-fern species richness as plots exposed to the highest deer densities, on average (Figs 2 and 3).

Our results regarding deer effects on *Rubus* at first may appear to be at odds with previously reported browse preference and negative effects of deer on *Rubus* cover (e.g. Horsley, Stout & deCalesta 2003). However, the apparent positive relationship between former deer density and *Rubus* cover is driven by the one site that had been refenced for 3 year immediately prior to this study. At this site, it appears that *Rubus* responded to exclusion of deer across the entire site in combination with higher light levels (lower leaf area index) under black cherry (*Prunus serotina*)–dominated canopies typical of stands initiated under high deer density (Nuttle *et al.* 2011). Prior to fencing, fern cover at this site was very high in the higher deer density treatments (Horsley, Stout & deCalesta 2003 followed by personal observations). Although unfortunate from an experimental design perspective, the refencing of this one site provides some evidence that in the absence of deer browsing and at high light levels, *Rubus* may be able to grow through a dense fern layer and suppress it (an effect also noted by Horsley & Marquis 1983; see also de la Cretaz & Kelty 2002).

The present study is the first to experimentally show that elevated deer densities cause the formation and long-term persistence of dense fern layers in the understorey. Other studies have inferred causality based on correlations between regional deer density and the rise of fern-dominated understoreys, and some have shown increased deer density to have this effect in the shorter term (see e.g., Horsley & Marquis 1983; de la Cretaz & Kelty 1999; Horsley, Stout & deCalesta 2003; Royo & Carson 2006). Still others have documented deer density's effects in suppressing woody and other non-woody vegetation (see Introduction). de la Cretaz & Kelty (2002) briefly review the mechanisms by which deer browsing allows dense fern layers to develop: ferns (unpalatable to deer) grow and spread more slowly than woody species unless those woody species are browsed excessively by deer. Though in the stands we studied, overstorey trees were eventually able to establish under all deer density treatments, and basal area of overstorey trees retains no legacy of former deer density (Nuttle *et al.* 2011), the browsing regime under high deer densities delayed tree establishment, allowing ferns to flourish (Horsley, Stout & deCalesta 2003). Now, though basal areas are equivalent, overstorey tree species composition differs markedly from low to high deer density, and canopy density (leaf area index) is significantly negatively related to former deer density, possibly driven by lower tree species diversity and higher dominance by black cherry at higher deer densities (Nuttle *et al.* 2011). Hence, higher light levels that remain in stands exposed to higher deer densities in the past allow ferns to persist there (see Hill & Silander 2001) while lack of an interfering fern layer presumably allows forbs and seedlings to persist in stands initiated under lower deer densities. The confluence of these processes does not appear to be unique to this particular system – Coomes *et al.* (2001) cited evidence of 'expanded niche occupation' by several species of unpalatable ferns and shrubs in New Zealand that may prevent restoration of forest tree communities even after reduction in introduced deer herds.

Several lessons for management of forest communities are informed by this study. First, though deer density during stand initiation exerts a powerful filter especially on woody seedlings (negative) and ferns (positive), once the stand is established with a depauperate, fern-dominated understorey, reducing deer density alone will not restore understorey communities. We know this because depauperate understoreys with dense fern layers created under high deer density (> 20 deer km^{-2}) did not recover after the end of the experiment when they experienced a 50% reduction in landscape-scale deer densities (ca. 10–12 deer km^{-2}) for the ensuing 20 year. Only when deer were completely excluded and when light levels were high (i.e. under sparse-crowned black cherry) could *Rubus* out-compete an established fern layer. Foresters in the region commonly apply herbicide to kill recalcitrant fern layers to promote forest regeneration following timber harvest (Horsley & Marquis 1983; de la Cretaz & Kelty 2002; Engelman & Nyland 2006), and Ristau *et al.* (2011) showed in the context of shelterwood seed cuts, with their higher light conditions, that herbicide treatment in combination with deer exclusion also permits the restoration of diverse understorey herbaceous layers. Hence, the combination of higher light, low deer browsing and removal of ferns seems to allow herbaceous and woody seedling communities to recover. The current study suggests that when deer are completely excluded, a higher light environment (as seen

here under sparse, black cherry-dominated canopies) may allow *Rubus* to out-compete and suppress ferns even without herbicide, potentially opening a window for growth of other species as well.

In the absence of such management interventions, we expect the legacies of deer density during stand initiation exhibited here to persist as long as these stands exist. Results from these stands suggest alternative futures where landscape-scale deer populations are managed at various levels. They may also inform management of other forest systems worldwide where overabundant mammalian herbivores have contributed to the formation of dense, recalcitrant herb and shrub layers (see Royo & Carson 2006). As more diverse stands that establish under lower deer densities continue through the stem exclusion stage, we expect they will experience an understorey re-initiation stage (Oliver & Larson 1996) where their forb and seedling communities continue to develop and increase in cover. In contrast, stands that establish under higher deer densities will not experience understorey re-initiation because their fern-dominated understoreys will suppress seedlings even as canopies open up allowing further spread of ferns. It is this condition that is far more prevalent across wide areas of eastern North America with a history of high deer densities and that will likely require management beyond deer population control to remedy.

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