

Equivalence in the strength of deer herbivory on above and below ground communities

Jean-Philippe Lessard^{a,*}, W. Nicholas Reynolds^a, Windy A. Bunn^a, Mark A. Genung^a,
Melissa A. Cregger^a, Emmi Felker-Quinn^a, M. Noelia Barrios-Garcia^a,
Mary L. Stevenson^a, R. Michael Lawton^a, Claire B. Brown^a, Maggie Patrick^a,
Janet H. Rock^b, Michael A. Jenkins^c, Joseph K. Bailey^a, Jennifer A. Schweitzer^a

^a*Dept. of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, United States*

^b*Inventory and Monitoring Program, Great Smoky Mountains National Park, 1316 Cherokee Orchard Road, Gatlinburg, TN 37738, United States*

^c*Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907, United States*

Received 10 June 2011; accepted 23 November 2011

Abstract

Herbivores exert a strong influence on the species composition and richness of plant communities, but the magnitude of their effect on belowground communities remains poorly understood. While an increasing number of studies acknowledge the importance of documenting belowground effects of herbivores, very few of these evaluate variation in the strength of the response from aboveground to belowground communities. Our study documents the long-term consequences of sustained deer herbivory for plant and arthropod communities adjacent to 15 exclosures that have been in place since 1996. We hypothesized that herbivory would alter the composition and diversity of communities, but the strength of the effects of herbivory would weaken from plants, to leaf-litter invertebrates, and to belowground microarthropod communities. First, we found that herbivory negatively impacted plant seedling and sapling abundance and performance, reduced the abundance of ants and the taxonomic richness of arthropods in the litter layer and reduced the richness of soil microarthropod communities. Second, in contrast to our hypothesis, the magnitude of effect size did not vary among trophic levels, indicating that effects of deer herbivory cascade from plants to the leaf-litter and soil arthropod communities with equal strength. While much recent research has focused on how specific traits of plants may mediate the effects of herbivory on associated species, our results suggest that indirect effects of herbivory might influence many components of belowground communities.

Zusammenfassung

Pflanzenfresser üben einen starken Einfluss auf die Zusammensetzung und den Artenreichtum von Pflanzengemeinschaften aus, aber das Ausmaß ihres Einflusses auf Gemeinschaften des Bodens ist unklar. Während eine zunehmende Anzahl von Untersuchungen die Wichtigkeit, den Einfluss von Herbivoren auf den Boden zu dokumentieren, anerkennt, bestimmten nur

*Corresponding author. Present address: Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. Tel.: +45 35 32 12 18; fax: +45 35 32 12 50.

E-mail address: jplessard@bio.ku.dk (J.-P. Lessard).

wenige die Variation in der Stärke der Reaktion von den oberirdischen bis zu den unterirdischen Gemeinschaften. Unsere Untersuchung dokumentiert die langfristigen Konsequenzen von andauernder Beweidung durch Wild auf die Pflanzen- und Arthropodengemeinschaften in der Nähe von 15 Ausschlussflächen, die seit 1996 bestanden. Wir vermuteten, dass die Beweidung die Zusammensetzung und Diversität der Gemeinschaften verändern würde, aber die Stärke des Effekts sollte sich von Pflanzen- über Streubewohner- hin zu endogäischen Mikroarthropodengemeinschaften abschwächen.

Wir fanden, dass die Beweidung die Abundanz und Wuchsleistung von Pflanzensämlingen und Schösslingen negativ beeinflusste und die Abundanz von Ameisen, die taxonomische Vielfalt der Streubewohner sowie den Artenreichtum der Bodenmikroarthropoden verringerte. Im Gegensatz zu unserer Hypothese variierte die Effektgröße nicht mit der trophischen Ebene, womit angezeigt wird, dass der Einfluss der Wildbeweidung von den Pflanzen zu den Streu- und Bodengemeinschaften mit gleicher Stärke weitergeleitet wird. Während viele neue Studien sich darauf konzentrierten, wie spezifische Eigenschaften von Pflanzen die Effekte der Beweidung auf vergesellschaftete Arten modifizieren, legen unsere Ergebnisse nahe, dass indirekte Effekte der Beweidung viele Komponenten von Bodengemeinschaften beeinflussen können.

© 2011 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Aboveground to belowground linkages; Biodiversity; Conservation; Deer herbivory; Indirect effects; Arthropod communities; Standardized effect size

Introduction

Sustained herbivory profoundly and pervasively alters plant communities and associated animal communities (Huntly 1991; Côté, Rooney, Tremblay, Dussault, & Waller 2004; Martin, Stockton, Allombert, & Gaston 2010). Herbivores can consume up to 90% of the aboveground standing plant biomass (Polis 1999) leading to major shifts in ecosystem properties and forest successional trajectories (Ammer 1996; Côté et al. 2004; Harrison & Bardgett 2008). Selective browsing by deer has long-lasting effects on the relative dominance of plant species and the physical structure of forests (Côté et al. 2004). These chronic changes resulting from prolonged deer herbivory often trickle down to the detrital food web, modifying the structure of litter and soil communities and, consequently, interfering with soil nutrient dynamics (Wardle, Barker, Yeates, Bonner, & Ghani 2001; Harrison & Bardgett 2004; Veen, Olf, Duyts, & van der Putten 2010). In particular, intense levels of herbivory inflicted by deer alter physical and chemical properties of soils that influence ecosystem processes (Harrison & Bardgett 2004, 2008; Bailey et al. 2007). While there is a growing appreciation for aboveground to belowground linkages (Bardgett & Wardle 2010), few studies have simultaneously contrasted the magnitude of aboveground and belowground responses to ungulate herbivory.

Studies of plant-mammalian herbivore interactions have traditionally focused on the direct effects of herbivory on plant communities or on specific plant traits. However, a growing body of empirical evidence suggests that herbivores affect both aboveground (Bailey & Whitham 2003; Allombert, Stockton, & Martin 2005) and belowground communities (Bardgett, Wardle, & Yeates 1998; Kinnear & Tongway 2004; Veen et al. 2010). For example, the community structure of microorganisms and invertebrates in the litter and soil decomposer food webs are largely mediated by interactions with litter resource quantity and quality (Hobbie 1992; Wardle 2002; Bradford, Gancos, & Frost 2008), and

heterogeneity (Hansen 2000), which often fluctuate with herbivore-induced changes in plant community composition. The diversity of belowground communities is typically negatively impacted through these interactions (Wardle et al. 2001; Veen et al. 2010), which can have large effects on food web structure and organic matter dynamics.

Previous findings suggest that the effects of ungulate herbivory are uneven across trophic levels, and often decrease in strength from aboveground to belowground communities (Bardgett et al. 1998; Wardle et al. 2001). First, effects of deer herbivory on aboveground plant communities are consistently strong and negative whereas effects on soil organisms such as nematodes are either positive (Bardgett et al. 1998), negative (Veen et al. 2010) or neutral (Wardle et al. 2001). Second, the impact of deer herbivory on organisms living in the leaf-litter may be stronger than for organisms living in the soil layers (Wardle et al. 2001). For example, the response of the soil micro-food web to deer browsing may be weak and multidirectional, whereas the response of arthropods in the litter is consistently strong and negative (Wardle et al. 2001). Very few studies, however, have compared the relative strength of effects of herbivory across trophic levels.

Why might herbivore effects on plant communities be stronger than those on litter and soil arthropods? It could be that herbivore effects on plants are direct whereas those on soil and arthropod communities are indirect. Although there is no general agreement about the relative strength of direct and indirect effects, theoretical work suggest that direct effects need to be strong for any indirect effects to be detected (Wootton 1994). In this study we used deer exclosures that have prevented deer herbivory for 11 years to examine the relative strength of deer herbivory effects on above and belowground communities. While much is known about the response of plant communities to browsing mammals in this system (Griggs, Rock, Webster, & Jenkins 2006), it is unclear whether and how much these effects transfer to litter and soil communities. We hypothesized that (1) changes in the plant community lead to reductions in leaf litter

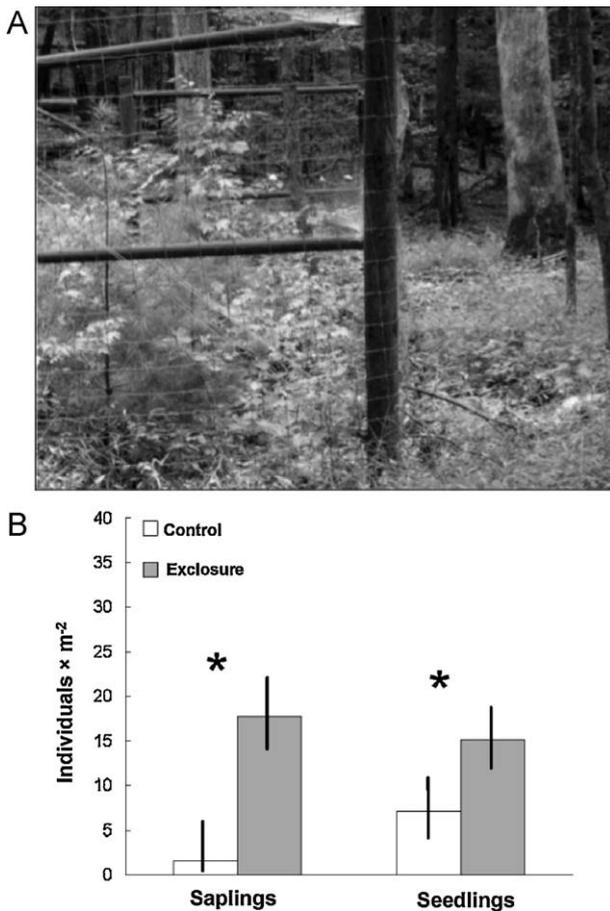


Fig. 1. Effects of deer herbivory on plant community structure. In general, tree seedling and sapling density and height is greater inside deer exclosures (established in 1996) than in browsed control plots in Great Smoky Mountains National Park (A). Mean (± 1 SE) seedling and sapling tree density tend to be greater in 11-year-old deer exclosures than in adjacent control plots (B). Asterisks indicate significant differences between control and experimental plots ($P < 0.05$).

accumulation and alter arthropod communities in the litter and soil, and (2) the strength of the effect of herbivory weakened from plant to litter- and soil-arthropod communities.

Methods

Study sites

We conducted this study using 11-year-old deer herbivore exclosures in Cades Cove, Great Smoky Mountains National Park (GSMNP), TN (N 35°35'39" W 83°50'30"; Fig. 1A). Cades Cove is a 2400 ha cultural landscape that is maintained by the National Park Service (NPS) to preserve the agricultural fields, historic structures, and woodlots that existed prior to the creation of the Park (see Webster, Jenkins, & Rock 2005, Webster, Rock, Froese, & Jenkins, 2008 for area history). Although the estimated pre-settlement population density of deer in the Cove was low (~ 5 deer/km²), after creation of GSMNP in 1940 and the cessation of hunting

the population rose to a peak of 43 deer/km² in the late 70s and are currently estimated to be around 35 deer/km² (Griggs et al. 2006).

In the fall of 1996, a total of 15 deer exclosures were established within Cades Cove in three forested sites located between 2 km to 4 km from one another (see Appendix A). Each site contains five deer exclosures that prevented herbivory and five browsed control plots, with continued herbivory; there were no non-deer affected controls. The exclosures are 12 m \times 12 m (2.5 m tall) and are constructed of heavy-gauge woven wire fencing. To avoid potential effects of the fencing on biotic and abiotic measurements, a 10 m \times 10 m plot was sampled within the exclosures, leaving a minimum 1 m buffer between sampling areas and the exclosure fence. Unfenced paired control plots are also 10 m \times 10 m and are located 10 m from each exclosure.

Community assessments

In September 2007, we inventoried seedling, sapling and overstory plant communities, litter arthropods, and soil microarthropods from deer exclosures and control plots (with variable sampling regimes across sites). We counted the number of seedling, saplings and trees in all exclosure and control plots across the 3 sites. We recorded the species identity, height, and basal diameter of each tree seedling (< 1.4 m tall) in two randomly selected 0.5 m \times 1 m quadrats within each exclosure and control plots at two of the sites. We also recorded the species identity and diameter at breast height (dbh; 1.37 m) of each sapling (dbh ≥ 1 cm and ≤ 10 cm) and overstory (dbh > 10 cm).

To investigate the abundance, richness and composition of litter arthropods, we collected leaf-litter from a 0.25 m² quadrat in the center of each control and exclosure plot at two of the sites. In each quadrat, we collected and sifted all the leaf-litter through a 1 cm mesh wire sieve. The sifted leaf-litter was placed in a mini-Winkler sack for 48 h to extract litter arthropods (as in Lessard, Sackett, Reynolds, Fowler, & Sanders 2011). Arthropods were preserved in 95% ethanol until they were counted and identified to the level of order or family.

Additionally, we investigated soil microarthropod abundance, richness, diversity, and composition to order or family level. We collected three soil cores (15 cm deep, 3 cm diameter) within each 0.25 m² leaf-litter quadrat at two of the sites. Microarthropods were extracted from soil samples with high-gradient Tullgren funnels for 7 days at 15 °C (Crossley & Blair 1991). Tullgren funnels dried the soil cores, which induced the microarthropods to migrate downward into 95% ethanol. All microarthropod specimens in each soil core were counted and identified.

Statistical analyses

We estimated abundance by counting the number of individuals of seedlings, saplings, trees and arthropods. Then

we estimated observed richness by counting the number of species (or the number of orders for litter arthropods) of each targeted taxon. We also used PRIMER-E (Version 6.1.6) to estimate rarefied richness. Individual-based rarefaction corrects species richness values for differences in the number of individuals sampled by using a re-sampling procedure to estimate species richness if an equal number of individuals had been sampled in each plot (Gotelli & Colwell 2001). We then used the Chao2 richness estimator, which provides an estimate of the actual number of species present in a plot (Chao & Bunge 2002). This is particularly useful for hyperdiverse taxa such as arthropods, which are seldom sampled to completion, but is not necessary for comparing plant species richness. In addition, we assessed the effects of deer herbivory on arthropod diversity using the Shannon diversity index (\ln), which gives an estimation of both the number of species and the degree of evenness in species' relative abundance. Due to the low sample size and paired sampling design of this study, we do not differentiate for sites in our analyzes and used paired t -test to assess whether there were significant differences in abundance and richness of plant and arthropods in paired enclosure and control plots.

We used non-metric multidimensional scaling (NMDS) based on Bray–Curtis similarity matrices generated with abundance data to describe differences in plant and arthropod community composition between control and enclosure plots. We used NMDS to quantify differences in species composition rather than other ordination techniques because it is statistically robust even with a small sample size. Paired analyses for tree and arthropod community composition were performed using the NMDS axis 1 scores for each plot (Shuster, Lonsdorf, Wimp, Bailey, & Whitham 2006) in paired t -tests.

We used a meta-analysis approach to address the hypothesis that the effects of herbivory would decrease in strength from plants to litter and soil communities. Meta-analysis is a statistical method for combining the results from separate tests to address the same research question, in order to estimate the mean effect size and identify the factors that influence the magnitude and direction of the effect (Gurevitch & Hedges 1999). We used the mixed effects model in MetaWin 2.1 (Rosenberg, Adams, & Gurevitch 2000) to summarize coefficients and perform the meta-analysis (see Appendix B).

Results

Seedlings inside the deer enclosures were 44% taller ($t_{(9)} = 3.01$, $p = 0.01$) and had 51% larger basal diameters ($t_{(9)} = 2.46$, $p = 0.04$) than seedlings in browsed control plots. Seedling density was 53% higher within the deer enclosures than in browsed control plots ($t_{(14)} = 2.23$, $p = 0.04$; Fig. 1B). Seedling species richness (corrected for density: $t_{(9)} = 2.09$, $p = 0.08$, observed: $t_{(9)} = 1.56$, $p = 0.15$) and community

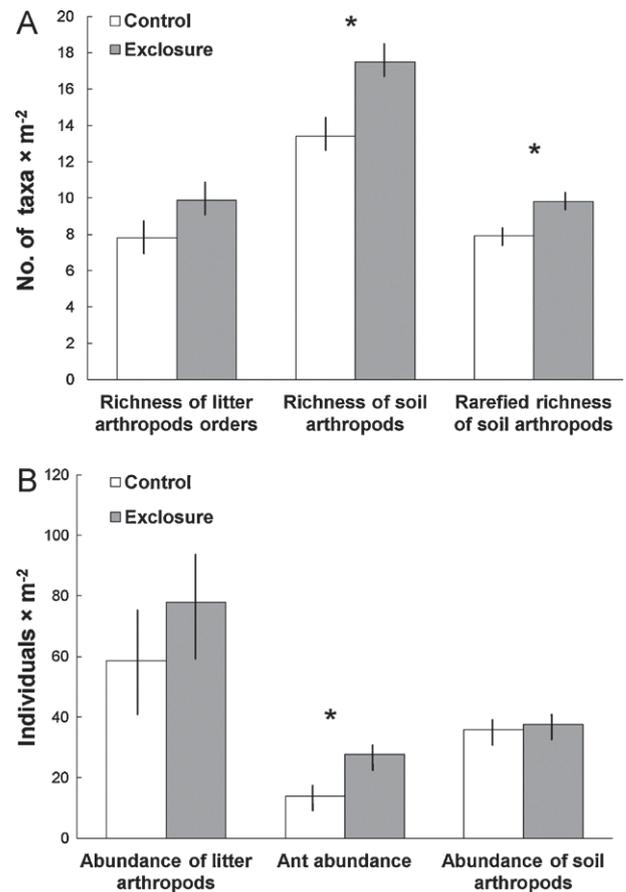


Fig. 2. Mean (± 1 SE) litter arthropod abundance did not differ between treatments while the order richness of litter arthropods and the abundance of ants were higher inside deer enclosures than browsed control plots (A). Mean microarthropod abundance (± 1 SE) was not affected; mean microarthropod species richness (± 1 SE) was higher in deer enclosures (B). Asterisks indicate significant differences between control and experimental plots ($P < 0.05$).

composition ($t_{(7)} = 1.9$, $p = 0.1$) did not differ inside and outside of the deer enclosures.

Sapling density was 91% higher inside deer enclosures than in browsed control plots ($t_{(14)} = 3.16$, $p < 0.01$; Fig. 1B). There was a marginally significant effect of deer herbivory on observed sapling richness (corrected for density: $t_{(9)} = 1.93$, $p = 0.09$, observed: $t_{(9)} = 2.18$, $p = 0.06$), but not on community composition ($t_{(3)} = 2.46$, $p = 0.09$). There were no differences in overstory tree density ($t_{(14)} = 0.47$, $p = 0.65$), richness ($t_{(9)} = 1.03$, $p = 0.33$), basal area ($t_{(9)} = 0.43$, $p = 0.68$), or community composition ($t_{(6)} = 1.96$, $p = 0.1$) between enclosure plots and browsed control plots.

Deer herbivory had negative, marginally significant, effects on litter arthropod order richness ($t_{(9)} = 2.16$, $p = 0.06$; Fig. 2A). We found no effect of deer herbivory on total abundance of litter arthropods ($t_{(9)} = 1.01$, $p = 0.3377$) or on community composition ($t_{(9)} = 1.25$, $p = 0.24$) even though leaf-litter depth was 35% greater inside enclosure plots than

in browsed control plots. However, we did find that the abundance of ants was higher inside the enclosure than in browsed control plots ($t_{(9)} = 2.75$, $p = 0.0283$; Fig. 2B).

Soil microarthropod species richness was 33% higher inside enclosures than in browsed control plots ($t_{(9)} = 4.17$, $p = 0.002$; Fig. 2A). Total estimated (Chao2, $t_{(9)} = 3.79$, $p = 0.004$) and corrected species richness (rarefied, $t_{(9)} = 4.19$, $p = 0.002$) of soil microarthropods were 22% and 24% higher in the enclosure plots than they were in browsed control plots. Soil microarthropods did not differ in abundance between treatments ($t_{(9)} = 0.34$, $p = 0.74$; Fig. 2B). Soil microarthropod species richness and diversity were 31% and 21% higher inside enclosure plots than in browsed control plots, respectively, while community composition was not affected (see Appendix C: Table 1).

Litter depth explained 32% of the variation in litter arthropod richness ($r^2 = 0.32$, $p = 0.009$; Fig. 3A) and 44% of the variation in soil arthropod richness ($r^2 = 0.44$, $p = 0.001$; Fig. 3A). Litter depth was not related to rarefied litter arthropod richness ($r^2 = 0.13$, $p = 0.44$), but explained 30% of rarefied soil arthropod richness ($r^2 = 0.30$, $p = 0.01$, Fig. 3A). Litter depth explained 45% of the variation in the abundance of litter arthropod ($r^2 = 0.45$, $p = 0.006$; Fig. 3B) and 25% of the variation in soil arthropod ($r^2 = 0.25$, $p = 0.02$, Fig. 3B). Finally, litter depth explained 24% of the spatial variation in spider abundance ($r^2 = 0.24$, $p = 0.03$).

The standard effect size of deer herbivory on plant community characteristics did not significantly differ from those of litter and soil arthropods (Model $Q_b = 11.31$, $p = 0.26$; Fig. 4). The effect of deer herbivory was strong (seedlings = 1.54; saplings = 1.72) and did not significantly weaken through litter (1.47) and soil (1.23) portions of this ecosystem (see Appendix C: Table 2 for more details). Note, however, that while effect sizes of plants were well above 1, those of litter or soils arthropods were either slightly above or not different from 1.

Discussion

Following a long-term deer exclusion experiment we found overall large negative effects of deer herbivory on plant, litter and soil community diversity. Specifically, the strength of deer browsing effects on litter and soil arthropod communities was equivalent to effects on plant communities. In contrast to our hypothesis that effects on the litter and especially soil arthropod communities would be weak relative to effects on aboveground plant communities, we found that the strength of the deer effects on arthropod communities was not significantly different than that on plants. We conclude that the effects of herbivory on litter and soil arthropods are likely indirect and mediated through reductions in the amount, and perhaps quality, of litter inputs to the decomposer food web on the forest floor (Bardgett & Wardle 2003; Wardle & Bardgett 2004).

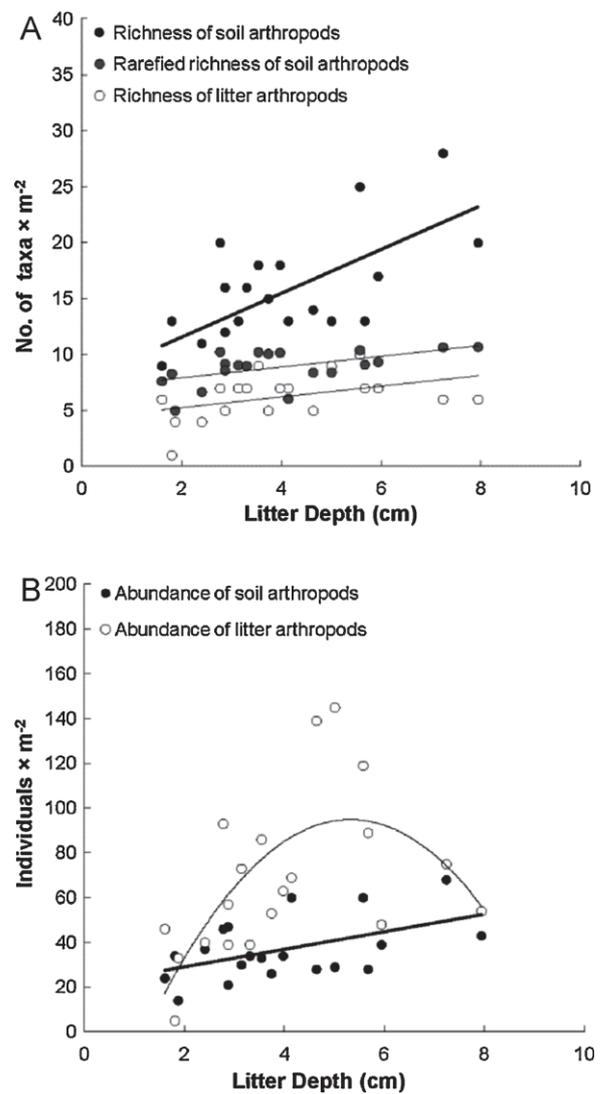


Fig. 3. Relationship between the diversity of arthropods and litter depth. Litter depth explained 25.2% of the variation in microarthropod abundance, 44.2% of the variation in observed microarthropod species richness and 29.5% of the variation in rarefied microarthropod richness across all plots (A). Each point represents the observed microarthropod species richness and the corresponding litter depth. Litter depth explained 45.4% of the variation in total litter arthropod abundance and 32.1% of the variation in litter arthropod order richness (B). Total rarefied litter arthropod richness was not related to litter depth.

Deer herbivory had strong effects on aboveground plant density. Consistent with previous findings of Webster et al. (2008), deer herbivory reduced seedling and sapling density and height in these same experimental plots. One consequence of chronic herbivory is that changes in plant community characteristics can spread across organization levels and alter overall forest structure by slowing growth and development of woody species, thereby reducing seedling recruitment into the sapling class (Frelich & Lorimer 1985; McInnes, Naiman, Pastor, & Cohen 1992; Stroh, Baltzinger,

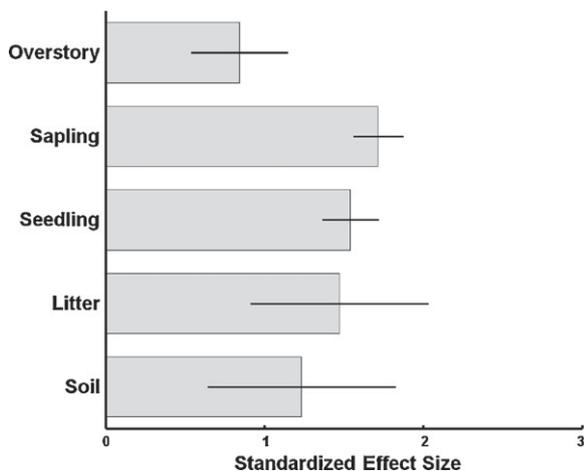


Fig. 4. Strength of the deer herbivory effects on aboveground and belowground communities. A total of 3–5 variables contributed to individual mean effect sizes (see Appendix C: Table 2). Bars represent mean effect size based on Z transformed r values and error bars represent 95% confidence intervals.

& Martin 2008). Such long-term changes in forest structure could further lead to alterations in associated communities (Cole, Buckland, & Bardgett 2005, 2008; Martin et al. 2010; Veen et al. 2010) and ecosystem processes such as nutrient cycling through changes such as litter quantity or quality (Wardle & Bardgett 2004).

Plant density, litter accumulation and the diversity of arthropods were higher in plots where deer were prevented from browsing. Arthropod communities are sensitive to experimental or herbivore-mediated (Bardgett et al. 1998; Bardgett & Wardle 2003) alterations in litter quantity (Osler, Korycinska, & Cole 2006), diversity (Hansen 2000; Reynolds, Crossley, & Hunter 2003), and litter quality (Hansen 1999). Here, we found a significant positive relationship between litter depth and litter arthropod richness across all experimental plots, supporting the hypothesis that herbivore-mediated reductions in litter quantity (or other factors co-varying with litter quantity) alters arthropod communities. Note that abundance-corrected arthropod richness was not related to litter depth indicating that spatial variation in arthropod abundance likely drives this positive relationship. These results are consistent with the findings of Kaspari and Yanoviak (2009), who found a positive relationship between the abundance of several arthropod taxa and litter depth across 26 forests stands in Peru and Panama. In particular, the abundance of large-bodied predators such as ants, staphilinid beetles and centipedes often increases with litter depth (Kaspari & Yanoviak 2009). Similarly, spiders in our study system increased in abundance with increases in litter depth, which is also consistent with findings from previous work (Uetz 1979; Bultman & Uetz 1982). Taken together our results support the idea that differences in the diversity of litter arthropods between browsed and un-browsed plots was

the result of a reduction in litter accumulation in browsed plots (Osler et al. 2006).

We found negative effects of deer herbivory on arthropod diversity in both the litter and soil layers, but several non-mutually exclusive mechanisms could lead to this pattern. As stated above, the effects of deer herbivory on soil communities may have been indirect and mediated by changes in litter quantity or quality. While in previous similar studies among-site differences in the intensity of herbivory by deer did not correlate with the strength of the response by soil and litter communities (e.g., Wardle et al. 2001), here we show a relationship between litter-depth and arthropod diversity across all sites. Thus deer herbivory may alter litter and soil communities via effects on litter inputs (Wardle et al. 2004). However, one caveat with such studies is the difficulty in teasing apart the direct and indirect effects of deer herbivory on litter and soil communities. For example, we cannot exclude the possibility that trampling by deer directly affected soil biota by altering the abiotic environment in the litter. Inputs of urine and feces from deer may also have directly influenced the heterogeneity of the soil environment (Augustine & Frank 2001) and associated faunal communities. In addition, physical disturbance via trampling alone or in combination with increased nutrient input could have direct effects on the soil biota (Battigelli, Spence, Langor, & Berch 2004; Cole et al. 2008; Mikola et al. 2009).

While previous studies have found weaker effects of herbivory in the soil relative to the litter layer, here the strength of these effects was equivalent. With the introduction of exotic ungulates in New Zealand, Wardle et al. (2001) found that herbivory affected all measured components of the mesofauna and macrofauna in the litter, but had weak and idiosyncratic effects on the taxa inventoried in the soil. Thus our results contrast with those of Wardle et al. (2001) since here the response of litter and soil organisms was strong and unidirectional. One reason for that discrepancy might be that the strength of the response in soil communities depends on the position of the particular organisms in the foodweb. Soil organisms in Wardle et al. (2001) consisted of microflora, nematodes, and tardigrades whereas soil organisms in our study were all arthropods (e.g., Pauropoda and Coleoptera). Nevertheless, the microbe-feeding and predatory nematodes in Wardle et al.'s (2001) study occupied trophic levels similar to soil arthropods in our study. Finally, it is worth pointing out that our results seem to indicate that although herbivory effects on soil and litter arthropods were not significantly different, there was a trend for stronger effects on litter than soil arthropods.

While several studies have outlined the mechanisms and occurrence of deer herbivory impacts belowground and aboveground (Wardle et al. 2001; Bardgett & Wardle 2003), studies that have quantified the relative strengths of these effects are rare. Our finding of equivalent impacts of herbivory on above and belowground communities challenges the hypothesis that herbivore impacts weaken as they spread through the food chain. Assessing the strength of disturbance

in various components of ecosystems requires statistical approaches that allow for making comparisons across habitat types and in regions varying in species richness. Owing to its capacity to estimate effect strength despite environmental idiosyncrasies, standardized effect sizes may thus be novel and powerful tools for quantifying the degree to which various forms of disturbance propagate across trophic levels. From a conservation and management perspective, it is important to note that the effects of deer herbivory can be strong (>1) both aboveground and belowground. Conservation effort should therefore consider impacts on both of these components, as well as the consequences of altering soil communities for the regulation of soil processes by ecosystem engineers such as ants (Wardle, Hyodo, Bardgett, Yeates, & Nilsson 2011).

Author contributions

All authors contributed to designing research; all authors except for JHR and MAJ sampled data; WNR, JKB and JAS analyzed data; JPL, JKB and JAS wrote the paper.

Acknowledgements

We thank Great Smoky Mountains National Park and the Department of Ecology and Evolutionary Biology at the University of Tennessee for their support. Our experiments complied with permitting requirements of the Department of the Interior's National Park Service and the laws of the United States of America. JPL was supported by NSERC doctoral scholarships and the Dept of Ecology and Evolutionary Biology at the University of Tennessee. JPL thanks the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.11.001.

References

- Allombert, S., Stockton, S., & Martin, J. L. (2005). A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology*, *19*, 1917–1929.
- Ammer, C. (1996). Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *Forest Ecology and Management*, *88*, 43–53.
- Augustine, D. J., & Frank, D. A. (2001). Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology*, *82*, 3149–3162.
- Bailey, J. K., Schweitzer, J. A., Rehill, B. J., Irschick, D. J., Whitham, T. G., & Lindroth, R. L. (2007). Rapid shifts in the chemical composition of aspen forests: An introduced herbivore as an agent of natural selection. *Biological Invasions*, *9*, 715–722.
- Bailey, J. K., & Whitham, T. G. (2003). Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos*, *101*, 127–134.
- Bardgett, R. D., & Wardle, D. A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, *84*, 2258–2268.
- Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground–belowground linkages*. Oxford, UK: Oxford University Press.
- Bardgett, R. D., Wardle, D. A., & Yeates, G. W. (1998). Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry*, *30*, 1867–1878.
- Battigelli, J. P., Spence, J. R., Langor, D. W., & Berch, S. M. (2004). Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. *Revue Canadienne De Recherche Forestiere*, *34*, 1136–1149.
- Bradford, M. A., Gancos, T., & Frost, C. J. (2008). Slow-cycle effects of foliar herbivory alter the nitrogen acquisition and population size of Collembola. *Soil Biology and Biochemistry*, *40*, 1253–1258.
- Bultman, T. L., & Uetz, G. W. (1982). Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia*, *55*, 34–41.
- Chao, A., & Bunge, J. (2002). Estimating the number of species in a Stochastic abundance model. *Biometrics*, *58*, 531–539.
- Cole, L., Buckland, S. M., & Bardgett, R. D. (2005). Relating microarthropod community structure and diversity to soil fertility manipulations in temperate grassland. *Soil Biology and Biochemistry*, *37*, 1707–1717.
- Cole, L., Buckland, S. M., & Bardgett, R. D. (2008). Influence of disturbance and nitrogen addition on plant and soil animal diversity in grassland. *Soil Biology and Biochemistry*, *40*, 505–514.
- Côté, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics*, *35*, 113–147.
- Crossley, D. A., & Blair, J. H. (1991). A high-efficiency, “low-technology” Tullgren-type extractor for soil microarthropods. *Agriculture, Ecosystems, and Environment*, *34*, 187–192.
- Frelich, L. E., & Lorimer, C. G. (1985). Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biological Conservation*, *34*, 99–120.
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*, 379–391.
- Griggs, J. A., Rock, J. H., Webster, C. R., & Jenkins, M. A. (2006). Vegetative legacy of a protected deer herd in Cades Cove, Great Smoky Mountains National Park. *Natural Areas Journal*, *26*, 126–136.
- Gurevitch, J., & Hedges, L. V. (1999). Statistical issues in ecological meta-analyses. *Ecology*, *80*, 1142–1149.
- Hansen, R. A. (1999). Red oak litter promotes a microarthropod functional group that accelerates its decomposition. *Plant and Soil*, *209*, 37–45.
- Hansen, R. A. (2000). Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology*, *81*, 1120–1132.

- Harrison, K. A., & Bardgett, R. D. (2004). Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest. *Soil Biology and Biochemistry*, *36*, 115–126.
- Harrison, K. A., & Bardgett, R. D. (2008). Impacts of grazing and browsing by large herbivores on soils and soil biological properties. In I. J. Gordon, & H. H. T. Prins (Eds.), *The ecology of browsing and grazing* (pp. 201–216). Springer.
- Hobbie, S. E. (1992). Effects of plant-species on nutrient cycling. *Trends in Ecology and Evolution*, *7*, 336–339.
- Huntly, N. (1991). Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, *22*, 477–503.
- Kaspary, M., & Yanoviak, S. P. (2009). Biogeochemistry and the structure of tropical brown food webs. *Ecology*, *90*, 3342–3351.
- Kinnear, A., & Tongway, D. (2004). Grazing impacts on soil mites of semi-arid chenopod shrublands in Western Australia. *Journal of Arid Environments*, *56*, 63–82.
- Lessard, J.-P., Sackett, T. E., Reynolds, W. N., Fowler, D. A., & Sanders, N. J. (2011). Determinants of the detrital arthropod community structure: The effects of temperature and resources along an environmental gradient. *Oikos*, *120*, 333–343.
- Martin, J. L., Stockton, S. A., Allombert, S., & Gaston, A. J. (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. *Biological Invasions*, *12*, 353–371.
- McInnes, P. F., Naiman, R. J., Pastor, J., & Cohen, Y. (1992). Effects of moose browsing on vegetation and litter of the Boreal forest, Isle Royale, Michigan, USA. *Ecology*, *73*, 2059–2075.
- Mikola, J., Setälä, H., Virkajarvi, P., Saarijarvi, K., Ilmarinen, K., Voigt, W., & Vestberg, M. (2009). Defoliation and patchy nutrient return drive grazing effects on plant and soil properties in a dairy cow pasture. *Ecological Monographs*, *79*, 221–244.
- Osler, G. H. R., Korycinska, A., & Cole, L. (2006). Differences in litter mass change mite assemblage structure on a deciduous forest floor. *Ecography*, *29*, 811–818.
- Polis, G. A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, *86*, 3–15.
- Reynolds, B. C., Crossley, D. A., & Hunter, M. D. (2003). Response of soil invertebrates to forest canopy inputs along a productivity gradient. *Pedobiologia*, *47*, 127–139.
- Rosenberg, M. S., Adams, D. C., & Gurevitch, J. (2000). *MetaWin: Statistical software for meta-analysis*. Sunderland, MA: Sinauer.
- Shuster, S. M., Lonsdorf, E. V., Wimp, G. M., Bailey, J. K., & Whitham, T. G. (2006). Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution*, *60*, 991–1003.
- Stroh, N., Baltzinger, C., & Martin, J. L. (2008). Deer prevent western redcedar (*Thuja plicata*) regeneration in old-growth forests of Haida Gwaii: Is there a potential for recovery? *Forest Ecology and Management*, *255*, 3973–3979.
- Uetz, G. W. (1979). Influence of variation in litter habitats on spider communities. *Oecologia*, *40*, 29–42.
- Veen, G. F., Olf, H., Duyts, H., & van der Putten, W. H. (2010). Vertebrate herbivores influence soil nematodes by modifying plant communities. *Ecology*, *91*, 828–835.
- Wardle, D. (2002). *Communities and ecosystems: Linking the above-ground and below-ground components*. Princeton, NJ: Princeton University Press.
- Wardle, D. A., & Bardgett, R. D. (2004). Human-induced changes in large herbivorous mammal density: The consequences for decomposers. *Frontiers in Ecology and the Environment*, *2*, 145–153.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*, 1629–1633.
- Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I., & Ghani, A. (2001). Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. *Ecological Monographs*, *71*, 587–614.
- Wardle, D. A., Hyodo, F., Bardgett, R. D., Yeates, G. W., & Nilsson, M.-C. (2011). Long-term aboveground and belowground consequences of red wood ant exclusion in boreal forest. *Ecology*, *92*, 645–656.
- Webster, C. R., Jenkins, M. A., & Rock, J. H. (2005). Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation*, *125*, 297–307.
- Webster, C. R., Rock, J. H., Froese, R. E., & Jenkins, M. A. (2008). Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. *Oecologia*, *157*, 497–508.
- Wootton, J. T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, *25*, 443–466.

Available online at www.sciencedirect.com

SciVerse ScienceDirect