

Short Communication

Special Issue: Interactions Between White-Tailed Deer and Invasive Plants in North American Forests

Introduction to the Special Issue: Ungulates and invasive species: quantifying impacts and understanding interactions

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Received: 19 September 2017 Editorial decision: 18 October 2017 Accepted: 7 November 2017 Published: 9 November 2017 Associate Editor: J. Hall Cushman

Citation: Blossey B, Gorchov DL. 2017. Introduction to the Special Issue: Ungulates and invasive species: quantifying impacts and understanding interactions. *AoB PLANTS* **9**: plx063; doi: 10.1093/aobpla/plx063

Abstract. White-tailed deer are emblematic ungulates that, due to anthropogenic modification of landscapes, currently occur at elevated densities. Elevated deer densities often co-occur with non-native plants, but it is not known if plant invasions are a consequence of deer impacts or occur independent of deer impacts on ecosystems, or whether these two stressors are synergistic. A colloquium on 'Interactions of white-tailed deer and invasive plants in forests of eastern North America' explored these topics at the 2016 annual meeting of the Botanical Society of America. Nine of those presentations are published in this special issue of *AoB PLANTS*.

Keywords: Facilitation; herbivory indirect effects; non-consumptive effects; Odocoileus virginianus.

Introduction

Ungulates make up the vast majority of large herbivores, and of the ~257 recognized species (http://www.ultimateungulate.com/ungulates.html) many are well-known charismatic or economically important species including horses, cattle, deer, pigs, giraffes, rhinoceros, goats and camels. Native ungulates around the world share living spaces and resources with many introduced ungulates and domestic livestock on public and private lands. Ungulate populations have fluctuated over time due to climate and hunting pressure, among other factors, and the causes of such changes and the consequences for shaping past and present-day ecosystems have been the focus of much recent ecological work and controversy (Miller *et al.* 2005; Donlan *et al.* 2006; Gill *et al.* 2009; Ripple and Van Valkenburgh 2010; Gill *et al.* 2012).

As ecologists, botanists, conservationists, policy makers or wildlife managers in the 21st century, we are facing, on the one hand, a conservation crisis due to rapid declines and endangerments of ungulate species primarily due to human exploitation (hunting), such as the Saiga antelope (*Saiga tatarica*) in Asia, the African rhinoceros species or the huemul (*Hippocamelus*

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© The Author(s) 2017. Published by Oxford University Press on behalf of the Annals of Botany Company. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/ licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited. bisulcus) in South America. On the other hand, populations of other native ungulate species have greatly increased due to human landscape transformations and predator elimination and trophic downgrading of ecosystems (Estes et al. 2011) in Europe, Australia, Japan and North America (Côté et al. 2004). Additionally, introduced ungulate species have often developed large populations; examples include deer and Himalayan tahr (Hemitragus jemlahicus) in New Zealand (Forsyth et al. 2010; Foster et al. 2014; Cruz et al. 2017) and several species of North American and Asian deer in Europe (Fuller and Gill 2001). The problems created by large native or introduced ungulate populations involve not just their direct effects through herbivory (Forsyth et al. 2010; Tanentzap et al. 2012; Foster et al. 2014; Perea et al. 2014), but also indirect effects through facilitation of other introduced and invasive species (Vavra et al. 2007; Eschtruth and Battles 2009; Nunez et al. 2013; Kardol et al. 2014; Shelton et al. 2014; Dávalos et al. 2015b, c; Wood et al. 2015; Shen et al. 2016; Russell et al. 2017).

The success of white-tailed deer in North America is a textbook example of wildlife management causing unintended consequences, and hence insights derived from this special issue may be applicable elsewhere. After Europeans arrived in North America, native deer predators (wolves, bears, mountain lions) were mercilessly shot and poisoned. Elimination of large predators was followed by near extinction of deer by recreational and market hunters. Establishment of state wildlife agencies in the early 1900s and conservation measures allowed deer to make a remarkable comeback on a landscape now devoid of their natural enemies, facilitated by forestry practices, agriculture and gardens (Halls 1984). Early local warning signs of negative ecosystem impacts of rapidly increasing deer herds (Leopold et al. 1947) were ignored since the return of deer was welcomed by hunters and furthered by the main philosophy of wildlife management agencies to achieve maximum sustainable yield (Jensen 1996; McCall et al. 1997; McCullough 2001), a concept quite similar to rangeland management for livestock production (Walker 1995). But this single species focus, and deer browse impacts in forests, gardens, orchards and fields, has resulted in contradictory objectives between those enjoying abundant wildlife (consumptive or non-consumptive interests) and those interested to protect their own fields or gardens or native species that are unable to flourish in the presence of high deer populations.

While experiments and studies across the range of white-tailed deer in North America have for a long time demonstrated that large deer populations create major direct economic (crops, timber, gardens) and ecological problems with impacts affecting entire food webs and ecosystem processes (Côté et al. 2004; Wardle and Bardgett 2004; McGraw and Furedi 2005; Nuttle et al. 2011; Schweitzer et al. 2014), recognition of their indirect, or nonconsumptive effects, is rather recent. For example, introduced plants may be symptoms of degradation facilitated by large deer populations (Vavra et al. 2007; Knight et al. 2009; Kalisz et al. 2014) or part of multiple stressor complexes simultaneously affecting many species (Fisichelli et al. 2013; Dávalos et al. 2015a, b). Thus, research on the impacts of invasive plants (e.g. Vila et al. 2011; Jauni and Ramula 2015) may yield misleading findings wherever the driver of undesirable changes in ecosystems is deer abundance and invasive plants are merely 'passengers' (MacDougall and Turkington 2005). It is also possible that there are synergistic impacts of deer and invasive plants, or that one stressor mitigates the impact of the other (Waller and Maas 2013). It is important to understand these interactions, particularly given that enormous management efforts are directed to lessen impacts of non-native invasive plant species (Foxcroft et al. 2014).

Key insights from the special issue

In August 2016, the Botanical Society of America convened a colloquium on 'Interactions of white-tailed deer and invasive plants in forests of eastern North America' at its annual meeting in Savannah, GA. Eleven speakers presented their research findings from studies carried out across the eastern and Midwestern United States. Nine of these investigators have published their findings in this special issue of *AoB PLANTS*.

Two papers in this special issue investigated whether and how deer promote invasion of non-native plants. Heberling et al. (2017) tested whether deer herbivory on native herbs promotes invasion of Alliaria petiolata, a non-native species avoided by deer (Knight et al. 2009). They found that deer herbivory on native herbs increased light availability compared to fenced plots, resulting in a higher maximum photosynthetic rate for A. petiolata. While one native herb (Maianthemum racemosum) also had greater photosynthetic rate in the presence of deer, this was countered by deer herbivory, and the other native, Trillium grandiflorum, had lower photosynthetic rates, as well as browse impacts, in the presence of deer. This study shows how physiological responses mediate the facilitation of A. petiolata invasion by high deer populations. Morrison (2017) staged an invasion of Microstegium vimineum to test whether deer facilitate the invasion of this annual grass in suburban forests, as well as explore the effects of both drivers on native plants. While fencing did not impede M. vimineum invasion, there was a significant interaction of deer and M. vimineum on native woody plants: cover of woody plants was lower

where deer had access and *M. vimineum* was introduced than in the other treatment combinations.

Three other papers examined combined and potentially interactive effects of deer and invasive plants on native plants. Owings et al. (2017) found that both deer and the invasive shrub Lonicera maackii reduced survival of seedlings of native oak and American chestnut (Castanea dentata) that were 'underplanted' in forests. While they found no significant interactions on seedling survival, L. maackii removal increased height of chestnut seedlings where deer were excluded but reduced height where deer were present, suggesting this invasive shrub may reduce deer browse on tree seedlings, as indicated by Peebles-Spencer and Gorchov (2017). Similarly, Bourg et al. (2017) used a replicated 2 × 2 factorial experiment across three forest stands to investigate effects of excluding deer and removing invasive plants. Deer exclusion had broad impacts on the plant community, resulting in higher native woody species richness and abundance and lower invasive plant abundance. Invasive plant removal had minimal direct effects, but only the combination of deer exclusion and invasive removal resulted in significantly greater native herbaceous richness. Averill et al. (2017) provide an integrated set of analyses on data pooled from 23 deer exclusion experiments to tease out deer effects on native and introduced plant species. Overall, deer reduced richness and abundance of native but not of introduced plants, resulting in greater proportions of introduced plants in communities. While certain invasive plant species were facilitated by deer, other invasives that are consumed by deer, including Rosa multiflora and Lonicera spp., respond rapidly to reduction in deer browse with an increase in cover. These three studies reveal that recovery or enhancement of populations of native plant species will not occur automatically by deer exclusion and removal of certain introduced species may also be warranted where they co-occur. However, invasive plant species removal without deer reduction is certain to fail in most instances or result in minor improvements.

Another paper explored the perspective of invasive plants impacting deer populations. Martinod and Gorchov (2017) provide evidence that the presence and abundance of introduced *L. maackii* establishes an abundant food source for deer that may elevate deer populations in ways that further reduce native plant populations. This effect is analogous to agricultural or ornamental plant subsidies, except that much of the herbivory occurs in early spring, when the invasive shrub has expanded leaves but native woody plants are still leafless. Thus, the direct competition often implied when researchers study effects of introduced on native plants, may instead be apparent competition facilitated by deer.

A second set of three papers examines the collection of evidence for deer impacts. Nuzzo et al. (2017) use two different deer reduction methods (fencing and culling) to assess recovery of native plant species. They assess both changes of the community (diversity) and of individuals and demonstrate that while some native plants may recover quickly, the species most threatened by deer show very slow recovery. Furthermore, they document that a focus on individuals in monitoring deer management efforts appears more likely to document benefits than focusing on community metrics like cover or diversity. These findings echo results of a meta-analysis of deer exclusion experiments focused on woody plants (Habeck and Schultz 2015). Blossey et al. (2017) introduced a new indicator species approach with repeat visits to marked planted red oak (Quercus rubra) individuals and showed that deer exclusion overrides effects of introduced plant species or other mortality factors (such as rodents or insects) in affecting performance of red oaks. This approach shifts the debate from a focus on ungulate numbers to ungulate impact, and this can help evaluate whether the chosen interventions are producing the desired outcomes. At the present time, this ecological assessment of outcomes is not routinely part of management but should be a required, including for management agencies (Decker et al. 2016).

Another methodological advance is reported by Erickson et al. (2017), who demonstrate a novel way to quantify deer consumption of native and introduced plants using DNA mini-barcoding. By extracting DNA from deer faecal pellets, amplifying the DNA corresponding to a chloroplast gene and comparing DNA sequences of amplified fragments to sequences of plant species in the study area, they were able to assess presence and frequency of plant species in diets of different individual deer. While individual faecal samples revealed each deer fed on numerous plant species, feeding was very selective, with some plants much more common in diets than their availability in the habitat, and others much less common or altogether lacking. Invasive plant species were included in both the set of species over-represented in deer diets (e.g. Eleagnus umbellata) and the set of species absent from faecal samples (e.g. Berberis thunbergii), indicating that deer preference for invasive plants differs greatly among plant species. This pattern is consistent with evidence from feeding trials (Averill et al. 2016).

Emerging from the findings of the studies in this special issue is further recognition of the overwhelming influence of deer in structuring present-day ecosystems and their trajectories, but with the added complication that different invasive plant species may respond differently to high deer populations. Most of the experiments reported in the studies in this special issue were designed and conducted in areas where invasive plant species and deer co-occur to assess their interactions. In these areas, deer exclusion alone will result in population declines of species that are avoided by deer and benefit from exotic earthworms, such as A. petiolata and M. vimineum which in turn are facilitated by deer (Dávalos et al. 2015c). However, culling deer or fencing areas where introduced species that are also consumed by deer, such as Lonicera spp. and R. multiflora, are abundant, may backfire and result in increased cover of these introduced species. Whether such increases are sustained, resulting in suppression of native plants by competition for light and nutrients, or temporary, due to increasing abundance of natives that in turn provide biotic resistance to plant invasion, requires long-term monitoring. While several deer exclosure experiments have been maintained for >10 years (Habeck and Schultz 2015; Averill et al. 2017), abundance of invasives has typically only been measured at one or two points in time (Shen et al. 2016; Averill et al. 2017). More long-term experiments, with periodic assessments, and low (not zero) deer densities are urgently needed. Over much of eastern and Midwestern North America deer reduction may need to be followed by control of invasive plants, at least those eaten by deer, to avoid recruitment problems for native species.

Conclusions

The contributions in this special issue offer further confirmation for what already is a strong scientific consensus on deer impacts, along with increasing evidence for facilitation of invasive plants by deer, via herbivory or non-consumptive mechanisms. The impacts of deer extend beyond the consequences of direct consumption, leading us to believe that consequences of high deer abundance may have been underestimated and are not yet fully recognized. Despite early warnings (Leopold et al. 1947) and decades of accumulating evidence of negative impacts of high deer populations, wildlife management agencies have been unsuccessful in structuring ungulate management in accordance with societal preferences (Jacobson et al. 2010; Smith 2011; Bengsen and Sparkes 2016). This failure points to problems in stewardship of natural resources to the benefit of all, not just special interest groups (Hare and Blossey 2014). It appears important to develop a new discourse that incorporates scientific evidence, stakeholder preferences and evidence-based management to develop approaches that safeguard all native species and prevent further erosion of plant biodiversity.

Sources of Funding

None declared.

Contributions by the Authors

The general framework of this manuscript was a collaboration by B.B. and D.L.G. The first draft was written by B.B. and revisions were made by both authors.

Acknowledgements

We thank the Ecological Section of the Botanical Society of America (BSA) for financial support of the Colloquium held at the 2016 BSA meeting. We thank the presenters at the Colloquium for stimulating presentations and discussion. Numerous external reviewers provided insightful and valuable comments to the manuscripts submitted for this special issue. We thank Hall Cushman, Chief Editor of *AoB PLANTS*, and Gail Rice, Managing Editor, for facilitating this special issue.

Conflicts of Interest

None declared.

Literature Cited

- Averill K, Mortensen D, Smithwick E, Kalisz S, McShea W, Bourg N, Parker J, Royo A, Abrams M, Apsley D, Blossey B, Boucher D, Caraher K, DiTommaso A, Johnson S, Masson R, Nuzzo V. 2017. A region-wide assessment of white-tailed deer on plant invasion. *AoB PLANTS* **9**:plx047; doi:10.1093/aobpla/plx047.
- Averill KM, Mortensen DA, Smithwick EAH, Post E. 2016. Deer feeding selectivity for invasive plants. *Biological Invasions* 18:1247–1263.
- Bengsen AJ, Sparkes J. 2016. Can recreational hunting contribute to pest mammal control on public land in Australia? *Mammal Review* **46**:297–310.
- Blossey B, Dávalos A, Nuzzo V. 2017. An indicator approach to capture impacts of white-tailed deer and other ungulates in the presence of multiple associated stressors. *AoB PLANTS* **9**:plx034; doi:10.1093/aobpla/plx034.
- Bourg N, McShea W, Herrmann V, Stewart C. 2017. Interactive effects of deer exclusion and exotic plant removal on deciduous forest understory communities. *AoB PLANTS* **9**:plx046; doi:10.1093/aobpla/plx046.
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics* **35**:113–147.
- Cruz J, Thomson C, Parkes JP, Gruner I, Forsyth DM. 2017. Longterm impacts of an introduced ungulate in native grasslands: Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand's Southern Alps. *Biological Invasions* **19**:339–349.

- Dávalos A, Nuzzo V, Blossey B. 2015a. Interactive effects of deer, earthworms and non-native plants on rare forest plant recruitment. *Biodiversity and Conservation* **187**:173–181.
- Dávalos A, Nuzzo V, Blossey B. 2015b. Single and interactive effects of deer and earthworms on non-native plants. *Forest Ecology and Management* **351**:28–35.
- Dávalos A, Simpson E, Nuzzo V, Blossey B. 2015c. Non-consumptive effects of native deer on introduced earthworm abundance. *Ecosystems* **18**:1029–1042.
- Decker D, Smith C, Forstchen A, Hare D, Pomeranz E, Doyle-Capitman C, Schuler K, Organ J. 2016. Governance principles for wildlife conservation in the 21st century. *Conservation Letters* 9:290–295.
- Donlan CJ, Berger J, Bock CE, Bock JH, Burney DA, Estes JA, Foreman D, Martin PS, Roemer GW, Smith FA, Soulé ME, Greene HW. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *The American Naturalist* **168**:660–681.
- Erickson D, Reed E, Ramachandran P, Bourg N, McShea W, Ottesen A. 2017. Reconstructing an herbivore's diet using a novel rcbl DNA mini-barcode for plants. *AoB PLANTS* **9**:plx015; doi:10.1093/ aobpla/plx015.
- Eschtruth AK, Battles JJ. 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. *Conservation Biology* **23**:388–399.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair AR, Soulé ME, Virtanen R, Wardle DA. 2011. Trophic downgrading of planet earth. *Science* **333**:301–306.
- Fisichelli NA, Frelich LE, Reich PB, Eisenhauer N. 2013. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. *Biological Invasions* 15:1057–1066.
- Forsyth DM, Wilmshurst JM, Allen RB, Coomes DA. 2010. Impacts of introduced deer and extinct moa on New Zealand ecosystems. *New Zealand Journal of Ecology* **34**:48–65.
- Foster CN, Barton PS, Lindenmayer DB. 2014. Effects of large native herbivores on other animals. *Journal of Applied Ecology* **51**:929–938.
- Foxcroft LC, Pysek P, Richardson DM, Genovesi P. 2014. Plant invasions in protected areas: patterns, problems and challenges. Dordrecht, The Netherlands: Springer.
- Fuller RJ, Gill RMA. 2001. Ecological impacts of increasing numbers of deer in British woodland. *Forestry* **74**:193–199.
- Gill JL, Williams JW, Jackson ST, Donnelly JP, Schellinger GC. 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* **34**:66–80.
- Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in north america. *Science* **326**:1100–1103.
- Habeck CW, Schultz AK. 2015. Community-level impacts of whitetailed deer on understorey plants in North American forests: a meta-analysis. *AoB PLANTS* 7:plv119; doi:10.1093/aobpla/ plv119.
- Halls LK (ed.). 1984. White-tailed deer: ecology and management. Harrisburg, PA: Stackpole Books.

- Hare D, Blossey B. 2014. Principles of public trust thinking. *Human* Dimension of Wildlife: An International Journal **19**:397–406.
- Heberling JM, Brouwer NL, Kalisz S. 2017. Effects of deer on photosynthetic performance of invasive and native forest herbs. *AoB PLANTS* **9**:plx011; doi:10.1093/aobpla/plx011.
- Jacobson CA, Organ JF, Decker DJ, Batcheller GR, Carpenter L. 2010. A conservation institution for the 21st century: implications for state wildlife agencies. *Journal of Wildlife Management* **74**:203–209.
- Jauni M, Ramula S. 2015. Meta-analysis on the effects of exotic plants on the fitness of native plants. *Perspectives in Plant Ecology, Evolution and Systematics* **17**:412–420.
- Jensen AL. 1996. Density-dependent matrix yield equation for optimal harvest of age-structured wildlife populations. *Ecological Modelling* **88**:125–132.
- Kalisz S, Spigler R, Horvitz C. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *Proceedings of the National Academy of Sciences of the United States of America* **111**:4501–4506.
- Kardol P, Dickie IA, St John MG, Husheer SW, Bonner KI, Bellingham PJ, Wardle DA. 2014. Soil-mediated effects of invasive ungulates on native tree seedlings. *Journal of Ecology* **102**:622–631.
- Knight TM, Dunn JL, Smith LA, Davis J, Kalisz S. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal* **29**:110–116.
- Leopold A, Sowls LK, Spencer DL. 1947. A survey of over-populated deer ranges in the United States. *Journal of Wildlife Management* **11**:162–177.
- MacDougall AS, Turkington R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems. *Ecology* **86**:42–55.
- Martinod K, Gorchov DL. 2017. White-tailed deer browse on an invasive shrub with extended leaf phenology meets assumptions of an apparent competition hypothesis. *AoB PLANTS* **9**:plx006; doi:10.1093/aobpla/plx006.
- McCall TC, Brown RD, Bender LC. 1997. Comparison of techniques for determining the nutritional carrying capacity for whitetailed deer. *Journal of Range Management* **50**:33–38.
- McCullough DR. 2001. Population manipulations of North American deer *Odocoileus* spp.: balancing high yield with sustainability. *Wildlife Biology* **7**:161–170.
- McGraw JB, Furedi MA. 2005. Deer browsing and population viability of a forest understory plant. *Science* **307**:920–922.
- Miller GH, Fogel ML, Magee JW, Gagan MK, Clarke SJ, Johnson BJ. 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* **309**:287–290.
- Morrison J. 2017. Effects of white-tailed deer and invasive plants on the herb layer of suburban forests. *AoB PLANTS* **9**:plx058; doi:10.1093/aobpla/plx058.
- Nunez MA, Hayward J, Horton TR, Amico GC, Dimarco RD, Barrios-Garcia MN, Simberloff D. 2013. Exotic mammals disperse exotic fungi that promote invasion by exotic trees. *PLoS One* **8**:e66832.
- Nuttle T, Yerger EH, Stoleson SH, Ristau TE. 2011. Legacy of topdown herbivore pressure ricochets back up multiple trophic levles in forest canopies over 30 years. *Ecosphere*. doi:10.1890/ ES1810-00108.00101.
- Nuzzo V, Dávalos A, Blossey B. 2017. Assessing plant community composition fails to capture impacts of white-tailed deer

on native and invasive plant species. *AoB PLANTS* **9**:plx026; doi:10.1093/aobpla/plx026.

- Owings C, Jacobs D, Shields J, Saunders M, Jenkins M. 2017. Individual and cumulative effects of white-tailed deer and an exotic shrub on artificial and natural regeneration in mixed hardwood forests. *AoB PLANTS* **9**:plx024; doi:10.1093/aobpla/ plx024.
- Peebles-Spencer JR, Gorchov DL. 2017. Are native tree seedlings facilitated by an invasive shrub where white-tailed deer are abundant? *Natural Areas Journal* **37**:540–548.
- Perea R, Girardello M, San Miguel A. 2014. Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. *Biodiversity and Conservation* **23**:1303–1318.
- Ripple WJ, Van Valkenburgh B. 2010. Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience* **60**:516–526.
- Russell MB, Woodall CW, Potter KM, Walters BF, Domke GM, Oswalt CM. 2017. Interactions between white-tailed deer density and the composition of forest understories in the northern United States. *Forest Ecology and Management* **384**:26–33.
- Schweitzer D, Garris JR, McBride AE, Smith JAM. 2014. The current status of forest Macrolepidoptera in northern New Jersey: evidence for the decline of understory specialists. *Journal of Insect Conservation* **18**:561–571.
- Shelton AL, Henning JA, Schultz P, Clay K. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management* **320**:39–49.
- Shen X, Bourg NA, McShea WJ, Turner BL. 2016. Long-term effects of white-tailed deer exclusion on the invasion of exotic plants:

a case study in a Mid-Atlantic temperate forest. *PLoS One* **11**:e0151825.

- Smith CA. 2011. The role of state wildlife professionals under the Public Trust Doctrine. *Journal of Wildlife Management* **75**:1539–1543.
- Tanentzap AJ, Kirby KJ, Goldberg E. 2012. Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. Forest Ecology and Management 264:159–166.
- Vavra M, Parks CG, Wisdom MJ. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management* **246**:66–72.
- Vila M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- Walker A. 1995. Grazing management and research now and in the next millennium. *Journal of Range Management* **48**:350–357.
- Waller DM, Maas LI. 2013. Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? *Forest Ecology and Management* **304**:296–302.
- Wardle DA, Bardgett RD. 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment* **2**:145–153.
- Wood JR, Dickie IA, Moeller HV, Peltzer DA, Bonner KI, Rattray G, Wilmshurst JM. 2015. Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. *Journal of Ecology* 103:121–129.