



Response of herbaceous layer species to canopy and soil variables in a central Appalachian hardwood forest ecosystem

Frank S. Gilliam

Received: 29 April 2019 / Accepted: 26 October 2019 / Published online: 11 November 2019
© Springer Nature B.V. 2019

Abstract Previous work has suggested that excess nitrogen (N) alters the degree to which forest canopy versus soil variables influence forest herb communities. This study tested the hypothesis that excess N would shift this influence on individual herb species from soil N availability to stand structural variables that determine light availability to the forest floor. Two watersheds at the Fernow Experimental Forest, West Virginia, USA were used: WS4 and WS3 as untreated reference and treatment watersheds, respectively. WS3 receives 35 kg N/ha/year via aerial application. Herb cover and composition was measured in seven permanent plots/WS from 1991, currently on-going. In 2011, soil moisture and N availability were measured in each plot, along with several variables of canopy structure. Backwards stepwise regression was used to determine relationships between herb cover/individual species and soil/canopy measurements. Herb cover varied spatially with soil resources on WS4, whereas cover varied spatially with canopy structure on WS3. Although results for total herb layer cover supported this hypothesis, results for individual herb species rejected it. This contrast was especially evident for

Rubus allegheniensis (blackberry), a nitrophilic species which increased with increasing soil N on both watersheds, but was not correlated with canopy structure on reference WS4, while being correlated with canopy structure on N-treated WS3. Excess N from atmospheric deposition has been shown to decrease plant biodiversity of impacted forests, especially in its effects on herbaceous layer communities. This work demonstrates that one of the mechanisms of such response is in N-mediated changes in the response of herb communities to soil resources and light availability.

Keywords Herbaceous layer · Forest canopy structure · Net nitrogen mineralization · Net nitrification

Introduction

A notable degree of past and recent research has focused on the variety of environmental factors that influence the herbaceous layer communities of forests. As has become increasingly realized, this forest stratum represents an importance to the structure and function of these ecosystems that is quite disproportionate to its diminutive stature, facilitating energy and nutrient flux and representing up to 90% of plant biodiversity (Gilliam 2007, 2014; Thrippleton et al.

Communicated by Claus Holzapfel.

F. S. Gilliam (✉)
Department of Biology, University of West Florida,
Pensacola, FL 32514, USA
e-mail: fgilliam@uwf.edu

2016). Thus, it is imperative to understand the nature of influences on herb layer dynamics, especially in the context of global change (De Frenne et al. 2013; Bellemare and Moeller 2014; Gilliam 2016).

Some of the earlier work in this area focused on the importance of environmental gradients within forests as primary drivers influencing herb layer communities, as well as on structural aspects and energy use efficiency of this stratum (Struik and Curtis 1962; Anderson et al. 1969; Zavitkovski 1976). Later work by Rogers in conifer and hardwood forests of the northern U.S. and Southern Canada (Rogers 1980, 1981, 1982, 1983, 1985) emphasized the high degree of interannual variability in herb cover, concluding that soil fertility was more influential than climate on forest herb communities.

Work in other forest types and using different methodology has yielded quite contrasting results. As part of the classic Hubbard Brook Study, Reiners (1992) reported a detailed chronology of 20 year of vegetation recovery following clearcutting and herbicide treatment, demonstrating that post-disturbance reorganization was largely influenced by light. High light-requiring species, e.g., *Rubus* spp., increased in abundance rapidly following cessation of herbicide treatment, but decreased just as rapidly during canopy re-initiation.

Certainly, light and soil resources are continually required by herb layer species; thus, neither factor should be considered as a sole driver in determining the structure and composition of forest herb communities (Bartels and Chen 2010; Walter et al. 2016). Among essential resources, light availability is spatially and temporally the most dynamic, passing through the forest canopy to the forest floor as sunflecks (Neufeld and Young 2014). Such spatial heterogeneity has been found to have a profound effect on herb richness and cover in forests (Reich et al. 2012; Kumar et al. 2018a, b). On the other hand, soil conditions, especially fertility, are not only often spatially heterogeneous, but this heterogeneity can maintain high species diversity of herb communities (Hutchings et al. 2003; Laliberté et al. 2013).

The light environment of the forest floor is primarily determined by variation in forest canopy structure (Atkins et al. 2018), including seasonal changes in foliar cover in deciduous stands (Neufeld and Young 2014) and changes over successional time. Once largely measured via satellites, such as Landsat

Thematic Mapper imagery (Jasinski and Crago 1999), a more recent technique using LiDAR technology with hand-held instrumentation allows for more detailed stand structural measurements at the smaller spatial scale of individual sample plots (e.g., 100–400 m²) (Lefsky et al. 2002; Parker et al. 2004a). Common measurements include local outer canopy height, rugosity ('roughness'), canopy area index, and gap fraction (see Atkins et al. 2018 and Methods for further description of these variables). In addition to numerous studies that have quantified these stand structural variables with applications toward the light environment (Aiba et al. 2013), others have linked them to forest microclimate and gas exchange (Parker et al. 2004b), energy flow and net primary productivity (Hardiman et al. 2011, 2013), management effects (McMahon et al. 2015), and forest greenness (LaRue et al. 2018).

Natural and anthropogenic disturbances can alter the relative degree of influence that soil and light environments can exert of forest herb communities (Roberts 2004; McMahon et al. 2015). Recent work on hardwood forests at the Fernow Experimental Forest (FEF), West Virginia, has suggested, via on-going watershed-scale manipulations for over a quarter century, that excess nitrogen (N) can shift the importance of soil fertility versus light in controlling spatial pattern in herb cover. Despite that N deposition, especially oxidized N, has declined throughout the eastern United States since around 1990, many sites still exhibit symptoms of N saturation (Peterjohn et al. 1996; Gilliam et al. 2019). At FEF, both canopy structure and soil resources variables (N availability and moisture) were quantified in samples plots wherein cover and diversity of the herb community was also measured. Herb cover on the untreated reference watershed varied with available soil N, whereas cover on the N-treated watershed varied with stand structural variables that affect the light environment of the forest floor. Herb community diversity, however, was influenced by neither stand nor soil variables (Gilliam 2019).

As that study did not include the responses of individual herb layer species to overstory structure and soil resources, the purpose of this study is to examine these relationships. More specifically, the following hypothesis is addressed, based on findings regarding total herb cover: Excess N shifts the control on herb layer species from soil N fertility to stand structure.

Methods

Study site

The research site for this study was the Fernow Experimental Forest (FEF), Tucker County, West Virginia (39°03'15" N, 79°49'15" W). This is part of a long-term study to determine the effects of chronic additions of N on central Appalachian hardwood forests (Adams et al. 2006). Fernow Experimental Forest is within the unglaciated Allegheny Plateau, occupying approximately 1900 ha area of the Allegheny Mountain section. Annual precipitation for this site averages ~ 1430 mm, generally higher in the growing season and increasing with higher elevations (Gilliam et al. 2018a, b).

Three watersheds are used in the broader, long-term study, of which two are employed for the current work: WS3, serving as the treatment watershed, and WS4, serving as reference watershed. Aerial applications of (NH₄)₂SO₄ to WS3 began in 1989 and remain on-going. These are made three times per year: March and November applications are 33.6 kg/ha of fertilizer, or 7.1 kg/ha of N, whereas July applications are 100.8 kg/ha fertilizer (21.2 kg/ha N). Stands on WS3 are ~ 50 years old and even-aged, following clearcutting. WS4 supports even-aged stands > 100 years old following harvesting.

Forest stands on these watersheds are mixed hardwoods, with dominant species including sugar maple (*Acer saccharum* Marsh.), sweet birch (*Betula lenta* L.), American beech (*Fagus grandifolia* Ehrh.), yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and northern red oak (*Quercus rubra* L.) (Kochenderfer 2006). At the initiation of sampling in 1991, species composition of the herbaceous layer was quite similar between watersheds, despite differences in stand age, including species of *Viola*, *Rubus*, seedlings of striped maple *Acer pensylvanicum* L. and red maple *A. rubrum* L., and a minor component of mixed ferns (Gilliam et al. 2016b).

Field methods

As part of long-term, on-going studies, cover of individual herb layer species was determined visually within five circular 1-m² sub-plots within each of seven circular 0.04 ha permanent sample plots; see

Walter et al. (2015) for detailed description of methodology. All vascular plants ≤ 1 m in height in each subplot were identified to species or genus and estimated for cover. This has occurred in the first week of July throughout the on-going study, but data for this study were taken from 2011 sampling only. Similarly, soil sampling and analyses are currently on-going, as described in Gilliam et al. (2018a, b). Plots for soil sampling are paired with and immediately adjacent to vegetation plots. Soil analyses include soil moisture (%), extractable NH₄⁺ and NO₃⁻, and net N mineralization and nitrification. Soil moisture was determined gravimetrically, NH₄⁺ and NO₃⁻ were measured colorimetrically following 1N KCl extraction, and net N mineralization and nitrification were determined using *in situ* incubations using mineral soil only (O horizon excluded). This was taken to a 5-cm depth on a monthly basis, generally from May to September each year. For this study, data from July 2011 were used to align with the herb layer and forest canopy measurements (see below).

Forest canopy structural variables were measured in July 2011 with a Riegl LD90-3100VHS-FLP laser rangefinder (operating in first-return mode at 890 nm and 2 kHz, laser safety class I) mounted to the front of a frame at 1 m above the ground. This was manually pointed upward, making 2000 measurements per second. Collected data were transferred through a serial cable to laptop (Parker et al. 2004a, b). Locations of each range measurement were estimated from its sequence in the data file with constant walking speed. Distances between measurements typically were < 1 cm, with the spot size of the laser beam varying between 4 and 6 cm at the ranges measured.

Canopy structure data files were edited to identify out-of-range values (for example, when penetrating canopy openings to the sky) and eliminate spurious values. Edited files were processed through a program customized for grouping ranges horizontally, calculating vertical profiles (using methodology of MacArthur and Horn 1969), estimating surface area density using the overlap transformation, and assigning coordinates to each estimate. The utilized bins were 1 m in the horizontal and 1 m in the vertical. Resulting estimates refer to cube-shaped voxels of 1 × 1 × 1 m in the x, y, and z dimensions, respectively.

To be consistent with earlier work (i.e., Gilliam 2019), this study used the following canopy structural variables: canopy area index (CAI), local outer canopy

height (LOCH), rugosity, and gap fraction. Canopy area index is the total surface area density across all levels in a column through the canopy. Local outer canopy height represents the maximum surface height in a column, comprising the outer canopy surface across all columns. Rugosity in its most general sense is a measure of the small-scale variation in amplitude in the height of a surface; in this case, rugosity quantifies the “roughness” of the forest canopy, calculated as the standard deviation of the mean outer canopy height. The gap fraction is the fraction of horizontal locations without any canopy surface area directly above (one minus the “cover”) (Parker et al. 2004a, b; Atkins et al. 2018).

Data analysis

Backwards stepwise regression was used to assess the potential effects of both canopy structural and soil variables on individual species of the herb layer. This procedure eliminates variables from the proposed model (see below) sequentially until all remaining variables produce F statistics that are significant at a given level of probability, i.e., $p < 0.05$ (Zar 2009). This was used to identify canopy and/or soil variables that best explain spatial variation in cover of individual species with the following initial model:

$$Y = \text{moist} + \text{NH}_4^+ + \text{NO}_3^- + \text{Nmin} + \text{nit} + \text{CAI} \\ + \text{LOCH} + \text{gapfrac} + \text{rug}$$

where moist is soil moisture (%), NH_4^+ and NO_3^- are extractable soil NH_4^+ and NO_3^- ($\mu\text{g N/g soil}$), Nmin is net N mineralization ($\mu\text{g N/g soil/d}$), nit is net nitrification ($\mu\text{g N/g soil/d}$), CAI is canopy area index, LOCH is local outer canopy height (m), gapfrac is gap fraction, rug is rugosity, and Y is the dependent variable, namely cover (%) of individual herb layer species.

Of additional interest was the relationship between cover of herb layer species and individual canopy and soil variables. Thus, in addition to the multiple regression approach and using the same variables, simple linear relationships were examined between cover of the more dominant plant species in each watershed with whichever canopy or soil variables were of best fit ($p < 0.05$).

Results and discussion

Results of this study largely reject the hypothesis that cover of individual herb layer species is more influenced by soil N under ambient conditions and by stand structure under high N conditions. Far more species in untreated WS4 exhibited significant results ($p < 0.05$) for the backwards stepwise procedure used to elucidate these relationships than in N-treated WS3, and among all species analyzed, all but two species (*Acer pensylvanicum* and *Viola* spp.—hereafter, *Viola*—on WS3) had significant coefficients for both canopy structural and soil variables (Table 1). The wide discrepancy in numbers of significant species between watersheds (4 vs. 10 in WS3 vs. WS4, respectively) likely has arisen, at least in part, from the increased dominance of the nitrophilic species, *Rubus allegheniensis* (hereafter, *Rubus*), that has developed through nearly a quarter century of N additions to WS3 (Gilliam et al. 2016b). As *Rubus* increased in cover on WS3 > 20-fold (< 1% in 1991 to 18% by 2011), it may have masked the response to stand and soil variables of individual herb layer species that declined as a result of such increases. Species richness was essentially identical between watersheds at the beginning of the study in 1991, but was $\sim 30\%$ lower on WS3 by the time of sampling for this study in 2011. This is also consistent with earlier observations from this site regarding *Rubus* as ecosystem engineer, effectively redistributing subsoil nutrients to surface horizons. Gilliam et al. (2016a) found that not only was foliar Mn was 50% higher in *Rubus* on WS3 than in *Rubus* on WS4 (~ 6000 ppm vs. ~ 4000 ppm, respectively), but also that discreet patches of high soil Mn on WS3 only occurred in areas with high cover of *Rubus*. Indeed, Gilliam et al. (2018a, b) demonstrated that *Rubus* further concentrates Mn in post-senescent foliar litter by > 50%, nearing the level (i.e., 10,000 ppm) to meet the minimum criterion as Mn hyperaccumulator (van der Ent et al. 2013). The low tolerance of most forest herb species to high soil Mn (Nagajyoti et al. 2010; Kula et al. 2012) suggests that *Rubus* cover may have altered the spatial relationships of these species to spatial patterns of canopy structure and soil N.

Contributing to these results is that WS4 might be considered an ecologically ‘moving target’ in its use as reference watershed. That is, despite its status as an unmanipulated ‘control’ in watershed-level experiments at FEF, it has, in the past, experienced

Table 1 Results of backward stepwise regression for study watersheds at Fernow Experimental Forest, WV, beginning with the following initial model: $Y = \text{moist} + \text{NH}_4^+ + \text{NO}_3^- + \text{Nmin} + \text{nit} + \text{CAI} + \text{LOCH} + \text{gapfrac} + \text{rug}$, where Y is cover, moist is soil moisture, NH_4^+ is

extractable soil NH_4^+ , NO_3^- is extractable soil NO_3^- , Nmin is net N mineralization, nit is net nitrification, CAI is canopy area index, LOCH is local outer canopy height, gapfrac is gap fraction, and rug is rugosity

Watershed	Species	Canopy variables				Soil variables					r^2
		CAI	gapfrac	LOCH	Rug	Moist	NH_4	NO_3	Nmin	nit	
WS3	Cover	- 35.39		3.01							0.96
	ACPE				- 5.67						0.71
	PRSE		- 10.01			0.13			- 0.89		0.99
	RUAL			2.46					22.13		0.99
	VIOL									2.09	0.69
WS4	Cover						- 5.32	12.62			0.90
	ACPE				0.88			- 1.98			0.91
	ACRU			- 0.08		- 0.19			1.24		0.99
	FRAM		98.48	- 0.50							0.87
	LACA							3.72			0.94
	LITU						- 0.28	1.25			0.97
	QURU	- 3.47									0.64
	RUAL						2.13				0.75
	SMRO								- 8.61		0.68
	STPU			- 0.16					0.32		0.84
VIOL			- 0.27					1.75		0.97	

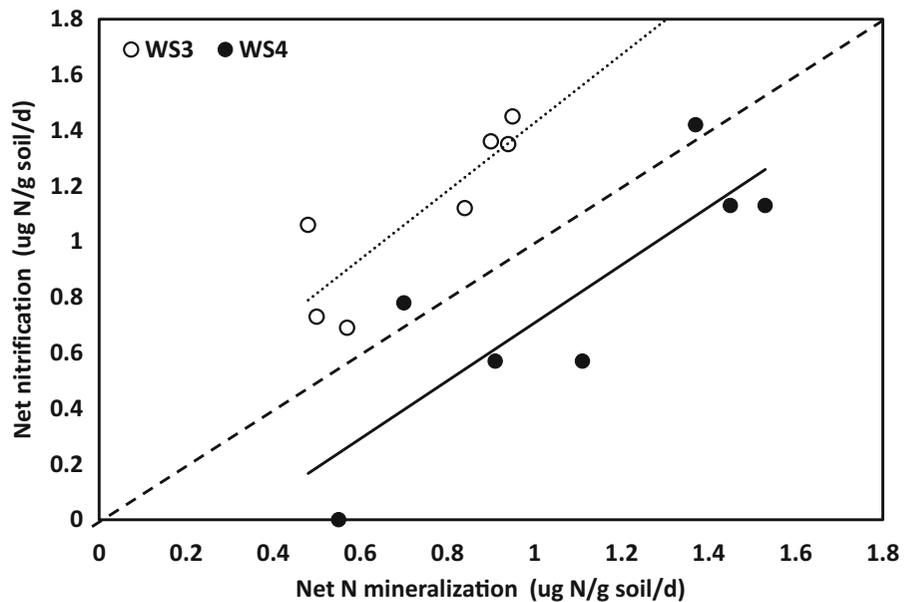
Values shown are coefficients for final significant ($p < 0.05$) model, along with r^2 for the final model of each species. Species codes are as follows: ACPE (*Acer pensylvanicum*), ACRU (*A. rubra*), FRAM (*Fraxinus americana*), LACA (*Laportea canadensis*), LITU (*Liriodendron tulipifera*), PRSE (*Prunus serotina*), QURU (*Quercus rubra*), RUAL (*Rubus allegheniensis*), SMRO (*Smilax rotundifolia*), STPU (*Stellaria pubescens*), and VIOL (*Viola* spp.). For reference, the final model for total herb layer cover is shown in bold

chronically elevated levels of N deposition, with wetfall amounts historically exceeding over 90% of National Atmospheric Deposition Program sites in the contiguous United States and Canada (Peterjohn et al. 1996; Adams et al. 2006). In fact, based on N data at the beginning of the on-going study in 1993, WS4 was identified by Peterjohn et al. (1996) as exhibiting several symptoms of being N saturated, including both high rates of net N mineralization and high relative net nitrification (i.e., the percent of N mineralization as nitrification). Data used in this study show that this was still evident in 2011 (Fig. 1). Regarding plant response, although not to the level observed on N-treated WS3, *Rubus* cover also increased from 1991 to 2011 on WS4—from ~ 0.5 to ~ 4%. Conversely, herb community richness increased during this period on WS4, in contrast to significant species loss on WS3 (Gilliam et al. 2016b), as has been reported in studies contrasting forest types from

throughout North America, Europe, and Asia (Gilliam 2006; Lu et al. 2010; Clark et al. 2013; Dirnböck et al. 2014; Simkin et al. 2016; Walter et al. 2017; Clark et al. 2019).

Contrasting patterns for *Rubus* between watersheds are compelling. On WS4, cover of *Rubus* was significantly related only to extractable NH_4^+ , which is actually consistent with the general hypothesis of N-mediated change in controlling factors for the herb layer. On WS3, however, cover was significantly related to both net N mineralization and LOCH, the latter of which has been found to be positively correlated with light availability to the forest floor (Aiba et al. 2013). These results support findings of Walter et al. (2016) that employed two separate, but coordinated, field studies to investigate the response of *Rubus* to variation in light and N availability in a factorial design by comparing relative cover of *Rubus* in (1) N-treated WS3 and another untreated watershed

Fig. 1 Net nitrification versus net N mineralization for individual sample plots on reference WS4 (closed symbols, solid line) and N-treated WS3 (open symbols, finely dashed line). Linear regression for WS4: $Y = 1.04X - 0.33$, $r^2 = 0.71$; linear regression for WS3: $Y = 1.23X + 0.20$, $r^2 = 0.74$. Shown also is a 1:1 reference line depicting a relative nitrification of 100%



at FEF (WS7) and (2) among N-fertilized and unfertilized experimental plots, with both approaches utilizing canopy openness as a covariate. The *ex situ* experiment used a two-way (2×3) factorial design, measuring leaf area with two levels of N and three of light. Both approaches revealed highly significant interactions between light and N in influencing *Rubus* cover, such that the effects of N availability on cover were significantly mitigated by availability of light (Walter et al. 2016).

Although the debate of organismic versus individualist concepts of plant communities was largely resolved decades ago (Clements 1936; Whittaker 1962), results of this study add further support of the individualistic concept, as established by Gleason (1926). That is, in spite of clear patterns of contrast between watersheds for herb cover as a whole (varying only with soil N on WS4 vs. only with canopy structure on WS3—Table 1), herb layer species varied individually and independently with respect both to each other and to N treatment. All species exhibited a significant relationship with at least one of the canopy or soil variables, but few showed similar patterns among themselves. Again, in contrast to the distinct N-mediated variation found for total herb cover, most species varied significantly with combinations of both canopy and soil variables (Table 1).

Finally, it merits reiterating the importance of *Rubus* as ecosystem engineer in how it has responded

to experimental additions of N on WS3, supporting conclusions of previous studies at this site (Gilliam et al. 2016b, 2018a, b). By definition, ecosystem engineers are species that alter the availability of resources for other species by altering biotic and abiotic factors, and modifying, maintaining, and creating habitats (Jones et al. 1994). As a nitrophilic species (Strik 2008) with an *R* life history (*sensu* Grime 2006), its proliferation in response to N on WS3 was not so surprising as that it did so under an intact forest canopy (Jobidon 1993). As it has increased in cover ~ 20 -fold over the quarter century of N treatments on WS3, it has not only altered resource availability to other species of the forest herb community, but has also redistributed Mn from the bottom of the rooting zone to surface soils at concentrations likely altering the success of other species. This work further underscores the complexity of mechanisms by which excess N can affect the most diverse of forest strata—the herbaceous layer.

Acknowledgements I am indebted to the excellent field assistance of several undergraduate and graduate students at Marshall University and West Virginia University. I am also pleased to thank Bill Peterjohn (West Virginia University) and Mary Beth Adams (USDA Forest Service) for field and logistical support, and am particularly indebted to Jess Parker (Smithsonian Environmental Research Center) for the LiDAR canopy measurements. The long-term support of the USDA Forest Service in establishing and maintaining the research watersheds is acknowledged. This research was funded in part

through United States Department of Agriculture (USDA) Forest Service, Fernow Experimental Forest, Timber and Watershed Laboratory, Parsons, W.V., under USDA Forest Service Cooperative Grants 23-165, 23-590, and 23-842 to Marshall University. Additional funding for this research was provided by USDA National Research Initiative Competitive Grants (Grant NRICGP #2006-35101-17097) to Marshall University and by the Long Term Research in Environmental Biology (LTREB) program at the National Science Foundation (Grant Nos. DEB-0417678 and DEB-1019522) to West Virginia University.

References

- Adams MB, DeWalle DR, Hom J (eds) (2006) The Fernow watershed acidification study. Springer, New York
- Aiba S, Akutsu K, Onoda Y (2013) Canopy structure of tropical and sub-tropical rain forests in relation to conifer dominance analysed with a portable LIDAR system. *Ann Bot* 112:1899–1909
- Anderson RC, Loucks OL, Swain AM (1969) Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50:255–263
- Atkins JW, Fahey RT, Hardiman BS, Gough CM (2018) Forest canopy structural complexity and light absorption relationships at the subcontinental scale. *J Geophys Res Biogeosci* 123:1387–1405
- Bartels SF, Chen HYN (2010) Is understory plant species diversity driven by resource quantity or resource heterogeneity? *Ecology* 91:1931–1938
- Bellemare J, Moeller DA (2014) Climate change and forest herbs of temperate deciduous forests. In: Gilliam FS (ed) *The herbaceous layer in forests of Eastern North America*, 2nd edn. Oxford University Press, New York, pp 460–493
- Clark CM, Morefield P, Gilliam FS, Pardo LH (2013) Estimated losses of plant biodiversity across the U.S. from historical N deposition from 1985–2010. *Ecology* 94:1441–1448
- Clark CM, Simkin SM, Allen EB, Bowman WD, Belnap J, Brooks ML, Collins SL, Geiser LH, Gilliam FS, Jovani SE, Pardo LH, Schulz BK, Stevens CJ, Suding KN, Throop HL, Waller DM (2019) Vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the U.S. *Nature Plants* 5:697–705
- Clements FE (1936) Nature and structure of the climax. *J Ecol* 24:252–284
- De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J et al (2013) Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci USA* 110:18561–18565
- Dirnböck T, Grandin U, Bernhardt-Römermann M, Beudert B, Canullo R, Forsius M, Grabner M-T, Holmberg M, Kleemola S, Lundin L et al (2014) Forest floor vegetation response to nitrogen deposition in Europe. *Glob Chang Biol* 20:429–440
- Gilliam FS (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *J Ecol* 94:1176–1191
- Gilliam FS (2007) The ecological significance of the herbaceous layer in forest ecosystems. *Bioscience* 57:845–858
- Gilliam FS (2014) Introduction: the herbaceous layer—the forest between the trees. In: Gilliam FS (ed) *The herbaceous layer in forests of Eastern North America*, 2nd edn. Oxford University Press, New York, pp 1–9
- Gilliam FS (2016) A novel mechanism to explain success of invasive herbaceous species at the expense of natives in eastern hardwood forests. *New Phytol* 209:451–453
- Gilliam FS (2019) Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity and shifts control from soil to canopy structure. *Forests* 10:1–13
- Gilliam FS, Billmyer JH, Walter CA, Peterjohn WT (2016a) Effects of excess nitrogen on biogeochemistry of a temperate hardwood forest: evidence of nutrient redistribution by a forest understory species. *Atmos Environ* 146:261–270
- Gilliam FS, Welch NT, Phillips AH, Billmyer JH, Peterjohn WT, Fowler ZK, Walter C, Burnham M, May JD, Adams MB (2016b) Twenty-five year response of the herbaceous layer of a temperate hardwood forest to elevated nitrogen deposition. *Ecosphere* 7(4):e01250. <https://doi.org/10.1002/ecs2.1250>
- Gilliam FS, May JD, Adams MB (2018a) Response of foliar nutrients of *Rubus allegheniensis* to nutrient amendments in a central Appalachian hardwood forest. *Forest Ecol Manag* 411:101–107
- Gilliam FS, Walter CA, Adams MB, Peterjohn WT (2018b) Nitrogen (N) dynamics in the mineral soil of a central Appalachian hardwood forest during a quarter century of whole-watershed N additions. *Ecosystems* 21:1489–1504
- Gilliam FS, Burns DA, Driscoll CT, Frey SD, Lovett GM, Watmough SA (2019) Decreased atmospheric nitrogen deposition in eastern North America: Predicted responses of forest ecosystems. *Environ Pollut* 244:560–574
- Gleason HA (1926) The individualistic concept of the plant association. *Bull Torrey Bot Club* 53:7–26
- Grime JP (2006) *Plant strategies, vegetation processes, and ecosystem properties*, 2nd edn. Wiley, Chichester
- Hardiman BS, Bohrer G, Gough CM, Vogel CS, Curtis PS (2011) The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology* 92:1818–1827
- Hardiman BS, Gough CM, Halperin A, Hofmeister KL, Nave LE, Bohrer G, Curtis PS (2013) The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *For Ecol Manag* 298:111–119
- Hutchings MJ, John EA, Wijesinghe DK (2003) Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* 84:2322–2334
- Jasinski MF, Crago RD (1999) Estimation of vegetation aerodynamic roughness of natural areas using frontal area density determined from satellite imagery. *Agric For Meteorol* 94:65–77
- Jobidon R (1993) Nitrate fertilization stimulates emergence of red raspberry (*Rubus idaeus* L.) under forest canopy. *Fert Res* 36:91–94
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386

- Kochenderfer JN (2006) Fernow and the Appalachian hardwood region. In: Adams MB, DeWalle DR, Hom JL (eds) The Fernow watershed acidification study. Springer, Dordrecht, pp 17–40
- Kula E, Hrdlicka P, Hedbavny J, Svec P (2012) Various content of manganese in selected forest tree species and plants in the undergrowth. *Beskydy* 5:19–26
- Kumar P, Chen HYN, Searle EB, Shahi C (2018a) Dynamics of understorey biomass, production and turnover associated with long-term overstorey succession in boreal forest of Canada. *For Ecol Manag* 427:152–161
- Kumar P, Chen HYN, Thomas SC, Shahi C (2018b) Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. *J Ecol* 106:1266–1276
- Laliberté E, Grace JB, Huston MA, Lambers H, Teste FP, Turner BL, Wardle DA (2013) How does pedogenesis drive plant diversity? *Trends Ecol Evol* 28:331–340
- LaRue EA, Atkins JW, Dahlin K, Fahey R, Fei S, Gough C, Hardiman BS (2018) Linking Landsat to terrestrial LiDAR: Vegetation metrics of forest greenness are correlated with canopy structural complexity. *Int J Appl Earth Obs Geoinf* 73:420–427
- Lefsky MA, Cohen WB, Parker GG, Harding DJ (2002) Lidar remote sensing for ecosystem studies. *Bioscience* 52:19–30
- Lu X, Mo J, Gilliam FS, Zhou G, Fang Y (2010) Effects of experimental nitrogen deposition on plant diversity in an old-growth tropical forest. *Glob Chang Biol* 16:2688–2700
- MacArthur RH, Horn HS (1969) Foliage profiles by vertical measurements. *Ecology* 50:802–804
- McMahon SM, Bebb DP, Butt N, Crockatt M, Kirby K, Parker GG, Riutta T, Slade EM (2015) Ground based LiDAR demonstrates the legacy of management history to canopy structure and composition across a fragmented temperate woodland. *For Ecol Manag* 335:255–260
- Nagajyoti PC, Lee KD, Sreekanth TVM (1992e) Heavy metals, occurrence and toxicity for plants. *Environ Chem Lett* 8:1992e16
- Neufeld HS, Young DR (2014) Ecophysiology of the herbaceous layer in temperate deciduous forests. In: Gilliam FS (ed) The herbaceous layer in forests of Eastern North America, 2nd edn. Oxford University Press, New York, pp 35–95
- Parker GG, Harding DJ, Berger M (2004a) A portable LIDAR system for rapid determination of forest canopy structure. *J Appl Ecol* 41:755–767
- Parker GG, Harmon ME, Lefsky MA, Chen J, Van Pelt R, Weiss SB, Thomas SC, Winner WE, Shaw DC, Franklin JF (2004b) Three-dimensional structure of an old-growth *Pseudotsuga-tsuga* canopy and its implications for radiation balance, microclimate, and gas exchange. *Ecosystems* 7:440–453
- Peterjohn WT, Adams MB, Gilliam FS (1996) Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. *Biogeochemistry* 35:507–522
- Reich PB, Frelich LE, Voldseth RA, Bakke P, Adair EC (2012) Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. *J Ecol* 100:539–545
- Reiners WA (1992) Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. *Ecol Monogr* 62:503–523
- Roberts MR (2004) Response of the herbaceous layer to natural disturbance in North American forests. *Can J Bot* 82:1273–1283
- Rogers RS (1980) Hemlock stands from Wisconsin to Nova Scotia: transitions in understorey composition along a floristic gradient. *Ecology* 61:178–193
- Rogers RS (1981) Mature mesophytic hardwood forest: community transitions, by layer, from east-central Minnesota to southeastern Michigan. *Ecology* 62:1634–1647
- Rogers RS (1982) Early spring herb communities in mesophytic forests of the Great Lakes Region. *Ecology* 63:1050–1063
- Rogers RS (1983) Annual variability in community organization of forest herbs: effect of an extremely warm and dry early spring. *Ecology* 64:1086–1091
- Rogers RS (1985) Local coexistence of deciduous-forest groundlayer species growing in different seasons. *Ecology* 66:701–707
- Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, Brooks ML, Cade BS, Collins SL, Geiser LH, Gilliam FS et al (2016) A continental analysis of ecosystem vulnerability to atmospheric nitrogen deposition. *Proc Natl Acad Sci USA* 113:4086–4091
- Strik BC (2008) A review of nitrogen nutrition of *Rubus*. *Acta Hort* 777:403–410
- Struik GJ, Curtis JT (1962) Herb distribution in an *Acer saccharum* forest. *Am Midl Nat* 68:285–296
- Thrippleton T, Bugmann H, Kramer-Priewasser K, Snell RS (2016) Herbaceous understorey: an overlooked player in forest landscape dynamics? *Ecosystems* 19:1240–1254
- van der Ent A, Baker AJM, Reeves RD, Pollard J, Schat H (2013) Hyperaccumulators of metal and metalloids: facts and fiction. *Plant Soil* 362:319–334
- Walter CA, Burnham MB, Gilliam FS, Peterjohn WT (2015) A reference-based approach for measuring the cover of forest herbs. *Environ Monit Assess* 187:657
- Walter CA, Raiff DT, Burnham MB, Gilliam FS, Adams MB, Peterjohn WT (2016) Nitrogen fertilization interacts with light to increase *Rubus* spp. cover in a temperate forest. *Plant Ecol* 217:421–430
- Walter CA, Adams MB, Gilliam FS, Peterjohn WT (2017) Non-random species loss in a forest herbaceous layer following nitrogen addition. *Ecology* 98:2322–2332
- Whittaker RH (1962) Classification of natural communities. *Bot Rev* 28:1–239
- Zar JH (2009) Biostatistical analysis, 5th edn. Prentice-Hall, Upper Saddle River
- Zavitkovski J (1976) Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. *Ecology* 57:694–706

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.