

SYNTHESIS OPEN ACCESS

Herbaceous Plants in Forest Ecosystems: One Hundred Fundamental and Applied Questions

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Received: 10 January 2026 | **Revised:** 2 June 2026 | **Accepted:** 15 July 2026

Coordinating Editor: Francesco de Bello

Keywords: forests | herbs | non-woody plants | research questions | understory plants

ABSTRACT

Aims: Herbaceous plants (herbs) found in the understory of forests contribute substantially to the biodiversity of these ecosystems, as well as being important socio-culturally, economically, and for advancing ecological theory. However, the ecology of herbs is less well understood compared with woody plants, despite evidence that herbs are physiologically and ecologically different. Similarly, herb research has focused on north temperate forests, with less information from forests in the tropics and Global South. Understanding this knowledge gap, and recognizing the critical importance of expanding and streamlining the scope of research on forest herbs, we set out to identify 100 fundamental and applied questions related to the ecology of this distinct plant group.

Methods: We first conducted a survey shared widely online with the ecological community, which generated a total of 130 questions. We then held a 3-day workshop involving invited herb researchers with expertise in various forest ecosystems, during which the questions were narrowed down through multiple rounds of discussion, revision, and rewording. For conceptual clarity, we then grouped the questions into 19 subject areas, although some questions are relevant to multiple subject areas.

Conclusions: These questions serve as a road map for future research in fundamental and applied herbaceous ecology in forested ecosystems. A common theme that emerged from this exercise was the need for standardized protocols to generate comparable data on terrestrial herbs from forests across the planet, including all forest types, biomes, and types of anthropogenic impacts. Research to address these questions will yield knowledge critical for advancing fundamental understanding of this ecologically important group of plants as well as the vital ecosystem services they provide, especially under global change, thus aiding better conservation and restoration policy and practice for forest ecosystems.

1 | Introduction

Understory herbaceous plants (i.e., “herbs”) account for up to 80% of the plant diversity in forest ecosystems (Gilliam 2007;

Spicer et al. 2020). They are central to the cultural practices of communities around the world (Hames and Hames 1976; Nakazono et al. 2004; Stepp 2018; Ralte et al. 2024), international export commodities (Nair 2019; Pizano 2023; Linares-Gabriel

For affiliations refer to page 10.

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et al. 2025), and are increasingly the focus of bioprospecting for active pharmaceutical ingredients (Mamadalieva et al. 2021; Chen et al. 2025). Despite their global ubiquity and importance, however, research on herbaceous plants is geographically biased to European and North American temperate and Mediterranean forests (Moss et al. 1910; Ellenberg 1988; Peterken 1993; Jefferson 2008; Taylor and Rowland 2010), and phylogenetically biased to certain taxa and functional groups (Vellend et al. 2003; Funk 2005). Overall, herbs remain historically understudied relative to woody plant species (Gilliam 2014a), and especially the trees that define forest structure (Chazdon et al. 2016). This deficit is particularly true for the tropics (Gentry and Dodson 1987; Filgueiras 2002; Costa 2004; Gilliam 2007; Linares-Palomino et al. 2009; Perea et al. 2022; Spicer et al. 2022) and the southern hemisphere (Coomes et al. 2005), where studies of understory herbaceous plants are rare (Massante et al. 2019).

The comparative lack of research on herbs outside of Europe and North America not only limits our understanding of their biology but also hinders their use as model systems for testing ecological, biogeographic, and evolutionary theory (but see, e.g., Hutchings and Price 1999; Vandepitte et al. 2009; Pfeiffer et al. 2019). This omission is important because there is increasing evidence that the diversity and dynamics of understory terrestrial herbs can be very different from those of woody plants. Herbs encompass a wider range of life forms than trees, with correspondingly unique life cycles and a larger variety of phenological adaptations and reproductive strategies (Raunkiaer 1934; Klimeš 2020). Herbs also have a wider range of life-history strategies, including clonality, plasticity, and hybridization, than do trees (Raunkiaer 1934; Winkler and Schmid 1995; Ellstrand et al. 1996). The biotic interactions of herbs with other organisms may also be different from those of trees (Haukioja and Koricheva 2000). As such, the drivers of herb diversity are likely different from those of woody plants (Whigham 2004; Schellenberger Costa et al. 2018; Radhamoni et al. 2023).

Herbs also differ from trees in aspects of many functional traits (Díaz et al. 2016; Šimová et al. 2018; da Silva Fortirer et al. 2023; Chen et al. 2024; Matsuo et al. 2024), as well as their potential sensitivity to climate change (Smith and Donoghue 2008; Smith and Beaulieu 2009; Zanne et al. 2014). Thus, herb populations may be useful indicators of impending shifts in forest composition and function that are not yet apparent in the tree communities (Webster et al. 2018). Expanding the breadth and depth of forest research to explicitly focus on herbs will therefore provide novel insights into the processes shaping plant population and community dynamics and the conservation of forest biodiversity (Filgueiras 2002; Spicer et al. 2022).

We present here 100 questions about terrestrial understory herbs in forest ecosystems, comprising key knowledge gaps and priorities for research. To arrive at these questions, we built on recent efforts (Gilliam 2007; Spicer et al. 2020, 2022) using an expert solicitation exercise similar to those conducted for other research foci, including ecology (Sutherland et al. 2013), conservation biology (Sutherland et al. 2009; Cooke et al. 2021), and belowground biology (Mammola et al. 2020). We aim to stimulate research, expand collaborations, and promote advances in our understanding of this speciose and ecologically critical component of forest biodiversity.

2 | Methods

Our goal was to identify and prioritize unanswered fundamental and applied research questions related to the dynamics and diversity of terrestrial understory herbs in forest ecosystems. As with similar exercises (Sutherland et al. 2009, 2013), we sought questions that could be answered by a small-to-medium research team with a moderately sized multi-year grant. Below, we describe the process for soliciting and finalizing the final list of 100 questions presented here.

2.1 | Stage 1: Survey and Collating Initial Questions

The preliminary list of questions was generated through an open community survey and expert solicitation (*sensu* Sutherland, Fleishman, et al. 2011; Sutherland, Goulson, et al. 2011). Using an online survey developed with the Qualtrics survey platform (Qualtrics, Provo, UT), we asked respondents to identify and prioritize the unanswered questions related to the dynamics and diversity of herbaceous plants in forested ecosystems across the world. For the purposes of this survey, “forested ecosystems” were defined as wet, moist, or dry forest and forest-related ecosystems (forests, woodlands, or savannas) from boreal, temperate, subtropical, or tropical climates, including urban, managed, fragmented, secondary, or primary forests in wetland, lowland, upland, montane/alpine terrains or islands.

Respondents were asked to submit questions that could be answered “over the course of several years by a small-to-medium sized research team with moderate research funding.” Survey participants were solicited through email listservs, social media, academic societies, and personal networks from the global community of experts on forest ecology, botany, horticulture, and related fields. We received a total of 37 completed survey responses, with 130 submitted questions (Appendix S1).

2.2 | Stage 2: Streamlining and Ranking of Questions

The preliminary questions were then debated, revised, and consolidated at a 3-day workshop attended by ecologists with expertise in fields, including plant or forest ecology, plant systematics, ecological sampling, statistical modeling, and herb conservation and management (April 12–15, 2023, Oak Spring Gardens, Upperville, VA, USA). Of the 37 initial survey respondents, 31 participated in the workshop (22 in person and nine online); the participants represented 20 institutions in seven countries (from North and South America, Africa, and Asia) and spanned the continuum of academic career stages (from graduate student to full professor) and had fieldwork experience in forest ecosystems around the world.

Prior to the workshop, the 130 questions from the initial survey were reviewed and pooled into preliminary categories by the workshop organizers (SQ, HV, MS, LC, and MD) and distributed to participants for review and proposed rewording and ranking (see Appendix S1 for details).

At the workshop, the participants spent 2 days further discussing, rewording, and ranking the 130 questions. This activity was done by dividing participants into several small interest groups, where working in parallel sessions they repeatedly discussed the questions related to their area of interest and worked on merging or rewording those. This was followed by plenary sessions where all workshop participants ranked the proposed new questions using an anonymous online form. After several iterations of this process, the participants reached consensus on the final list of 100 questions. The questions were then edited throughout the revision process.

2.3 | Caveats

Exercises such as this have limitations based on participant expertise, the questions submitted, and the identity and number of workshop participants (reviewed in Sutherland et al. 2009, 2013). Participation in turn depends on such factors as the financial support available for travel and the availability and resources of potential participants. Some of these limitations applied to our workshop as well, but they were offset in part by the now-ubiquitous adoption of online communication platforms that allowed scientists from around the world to participate in our workshop in real time. This technology helped ensure our discussions included the perspectives of participants at different career stages and with expertise on a broad range of topics, biomes, and taxa. We also acknowledge that important literature pertaining to the 100 questions posed here exists; however, it is impractical to review all relevant literature here, as it was not the primary goal of the paper.

3 | Results

We grouped the resulting 100 questions into 19 broad subject areas, summarized in Appendix S2. The numbering of questions within and across subject areas does not reflect their ranking of priority by the workshop members.

3.1 | Patterns and Drivers of Diversity and Distribution

We still lack data on the abundance, diversity, and distribution of herbs—and how this varies with spatial and temporal scale—for most of the world's forests (Spicer et al. 2022). Most work to date has focused on the temperate forests of northeastern United States (Curtis 1959; Amatangelo et al. 2014; Gilliam 2014b; Beck et al. 2022) and Europe (Verheyen et al. 2003; Mölder et al. 2008; Schulze et al. 2016; Bugno-Pogoda et al. 2021), whereas proportionately far fewer studies have been conducted in species-rich tropical forests and the southern hemisphere (but see, e.g., Gentry and Emmons 1987; Poulsen 1996; Costa 2006; Jones et al. 2006; Linares-Palomino et al. 2009; Cicuzza et al. 2013; Murphy et al. 2016), and especially tropical dry forests (Linares-Palomino et al. 2011; Radhamoni et al. 2023). Regardless of biome, relatively few studies use comparable methods (sensu Curtis 1959; Peet et al. 2012; Waller et al. 2012), which impedes cross-site comparisons of herb diversity and composition.

Generating comparable quantitative data using standard methods would transform our knowledge of the diversity and distribution of understory herbs in forests.

1. What are the patterns of forest herb diversity (taxonomic, functional, phylogenetic, and genetic) at local, regional, and global scales (alpha, beta, and gamma diversity), and how do these patterns differ from those documented for other plant life forms?
2. What are the evolutionary and biogeographic processes that shape the global distributions of forest herbs?
3. How do genetic diversity and population genetic structure vary within and among herb species, forest types, and at different spatial scales?
4. What are the drivers of state transitions for understory forest herb communities?

3.2 | Abiotic Drivers of Diversity and Distribution

Climate drives the distribution of plant biomes across the globe (Kleidon and Mooney 2000; Kreft and Jetz 2007; Fine 2015), as well as variation in species richness and composition (Fine 2015). Studies of tree communities point to strong effects of water and soil nutrients on diversity (Esquivel-Muelbert et al. 2017; Dattaraja et al. 2018), and the impact of such drivers on forest herbs is evident in available studies of understory diversity and community composition (Jones et al. 2006; Burton et al. 2011; Tian et al. 2023; Radhamoni et al. 2023, 2025; Geng et al. 2024; Deng et al. 2025) and of micro-scale heterogeneity within forests (Bratton 1976; Gilbert and Lechowicz 2004; Beck and Givnish 2021; Beck et al. 2022). There is also, however, evidence that light levels may be more important than water availability for herbs (Radhamoni et al. 2023). Addressing the knowledge gaps in our understanding of how abiotic factors influence forest herb communities is critical.

5. How do seasonal and spatial variation in light availability influence herb community diversity?
6. How does local-scale understory habitat heterogeneity in resources (e.g., microclimate, soil nutrients, and light) or substrate (e.g., tip-up mounds, burrows, and termite mounds) determine the diversity and dynamics of herb communities?
7. How does the relative importance of various drivers (light, water, and nutrient availability) differ between herbs and trees?
8. Does the relative importance of various drivers differ among global forest types and regions (e.g., tropical vs. Mediterranean, austroboreal vs. austrotropical, and upland vs. wetland forests)?

3.3 | Biotic Drivers of Diversity and Distribution

Competition with other herbs (Keddy and Shipley 1989), neighboring trees (Seghieri 1995), and shrubs (Ram and

Chawla 2024)—as well as their juvenile or sapling stages (Vandenberghe et al. 2006, 2008; Yin et al. 2023)—likely has a strong effect on herb diversity and distribution. Overstory trees have a major influence on the abundance, diversity, and composition of herbs (Berger and Puettmann 2000; Bartels and Chen 2012; Yu and Sun 2013; Veresoglou et al. 2017; Tölgyesi et al. 2018; Zhukov et al. 2019; Jia et al. 2022; Deng, Fang, et al. 2023; Wassel and Myers 2025). The same is true of interactions with soil biota, herbivores, pests, and pathogens (Fernandes et al. 2002; Rooney and Waller 2003; Shannon et al. 2012; Smith and Reynolds 2015; Koerner et al. 2018; Beck 2021; Havrdová et al. 2025). In contrast, herbs also have a significant effect on the recruitment and regeneration of trees (George and Bazzaz 1999; Coomes et al. 2005). Additional studies are needed to better understand the role of biotic interactions in shaping forest herb communities.

9. How do various competitive interactions (intraspecific, interspecific, or with other plant growth forms) shape the distribution and diversity of forest herbs?
10. What are the effects of overstory composition and traits on herbaceous diversity and dynamics?
11. How do soil biota (e.g., microbes, fungi, and invertebrates) influence the diversity, distribution, and community dynamics of forest herbs?
12. Does the concept of “foundational species” apply to the herb layer? Are there species whose effects are disproportionate to their relative biomass?
13. How do natural enemies (e.g., herbivores and pathogens) influence the diversity and distribution of understory herbs, and how does this vary across forest ecosystems?
14. Do herbivores drive long-term stable transitions to alternate herb communities?

3.4 | Community Assembly and Coexistence

Local species assembly of organisms, including that of plants, depends on the interplay of deterministic and stochastic processes with ecological and evolutionary significance (Fukami 2015; Vellend 2016; Barabás et al. 2018; Måren et al. 2018), whereas both niche and neutral processes influence species coexistence (Levine and HilleRisLambers 2009; Stump and Comita 2020). Conspecific negative density dependence (CNDD) is considered central to the coexistence of plant species (LaManna et al. 2017; Stump and Comita 2018); although there is ample evidence of CNDD's importance from studies with tree communities, similar studies with herbs are limited. Although CNDD is likely also to play a role in herb species coexistence, its relative importance may differ due to differences between herbs and trees in dispersal syndromes and distances and in their responses to abiotic conditions, disturbances, and biotic interactions (Burton et al. 2011; Barry and Schnitzer 2021).

15. How does the relative influence of various community assembly mechanisms differ among plant groups (e.g., herbs and trees) and among forest types?

16. Do growth–survival trade-offs allow herb survival in low-light environments?
17. To what extent is niche partitioning (e.g., light and soil) important for the coexistence of herb species?
18. How does the relative importance of deterministic versus stochastic processes in structuring herb communities change across environmental gradients and spatial scales?
19. Are patterns of forest herb community assembly consistent with competition–colonization trade-offs?
20. To what extent does CNDD influence the diversity, distribution, and coexistence of forest herb species?
21. Temporal niche partitioning plays an important role in facilitating the coexistence of temperate herbaceous plants (e.g., spring ephemerals, transient species, and core species); is this also the case in non-temperate forests?

3.5 | Interactions With Fungi and Other Microbes

The interactions of plants with soil microbes, including bacteria and fungi, drive fundamental processes, such as nutrient cycling (Marschner 2007; Churchland and Grayston 2014; Wang et al. 2025) and influence the structure and function of forests (Winsome et al. 2017; Stump and Comita 2018; Albornoz et al. 2022). Although most of these studies focus on trees (LaManna et al. 2017), herb–microbial interactions are not unknown. For example, temperate forest herbs form symbiotic associations with fungi (Rožek et al. 2019), and they influence soil fungal and bacterial communities (Wolfe et al. 2008; Chen et al. 2021; Stefanowicz et al. 2022; Zubek et al. 2024). Herbs may also host pathogenic and endophytic microbes (Qin et al. 2009), some of which they share with trees and shrubs (e.g., root-endophytic fungi; Toju et al. 2013). Some forest herbs are also myco-heterotrophic, as they extract carbon from fungal sources (Leake 2005). However, the species-, community-, and ecosystem-level importance of such interactions remains largely unknown, especially in tropical forests.

22. In what categories of microbial interaction do forest herbs engage, and how does the ecological function of these interactions vary across different forest ecosystems?
23. Which herbaceous species associate with mycorrhizal fungi, and how do patterns of association compare to those for trees or shrubs?
24. How specialized are herb–microbe interactions?
25. Do mycorrhizal associations with herbs influence individual fitness, community composition, and ecosystem function?

3.6 | Other Biotic Interactions

Although the performance of individual herbs and the dynamics of their populations are influenced by the plants and animals with which they interact, the reverse could also be true. For example, there is increasing awareness that herbs influence tree

regeneration (George and Bazzaz 1999; Coomes et al. 2005; Royo and Carson 2008; Elliott et al. 2015; Thrippleton et al. 2016). Herbs have also been model systems for the study of herbivory (Rooney and Waller 2003; Royo et al. 2010; Christopher et al. 2014; Faison et al. 2017), seed dispersal (Vellend et al. 2003; Rooney and Waller 2003; Myers et al. 2004; Warren and Bradford 2011; Blyth et al. 2013; Guiden 2017), pollination (Barrett and Helenurm 1987; Gandhi and Herms 2010), and other plant–animal interactions (Fernandes et al. 2002; Boulanger et al. 2018). However, studies of multiple interactions with the same herb species and comparative studies of biotic interactions across forest types and among plant groups remain a priority.

26. How do herb community composition and ground cover influence the recruitment and regeneration of tree seedlings and other plant groups in the understory?
27. How do the interactions between herbs and tree seedlings (from competitive to facilitative) vary along abiotic gradients?
28. How does abiotic variation influence plant–animal interactions in the herb layer?
29. Are herb–animal interactions more specialized than those of animals with woody plants or vice versa?
30. How do pollination, defense, and dispersal syndromes vary across herbaceous species and forest types?
31. To what extent do herbs and woody plants share pollinators and dispersers?
32. To what extent are aboveground versus belowground biotic interactions important to herbaceous plant fitness?

3.7 | Functional Traits

In recent decades, studies of variation in functional traits among individuals, species, and communities have guided a deeper mechanistic understanding of plant community assembly, succession, ecological strategies, and ecosystem function in forests (Lavorel and Garnier 2002; Mason et al. 2005; McGill et al. 2006; Bruelheide et al. 2018; Kemppinen et al. 2021; Kambach et al. 2023). Leaf traits associated with a trade-off between resource acquisition and stress tolerance (the leaf economics spectrum, LES) have received considerable attention (Wright et al. 2004). However, other key traits—especially root traits—remain conspicuously understudied (Chave et al. 2009; Roumet et al. 2016; Weemstra et al. 2016; Chelli, Klimešová, et al. 2024), or restricted to certain forest types and geographic areas (Petrauski et al. 2019). Herbs are distinguished from woody plants along trait axes associated with various other traits orthogonal and independent of the LES (Grime 2006; Díaz et al. 2016; Burton et al. 2017, 2020), and forests are distinguished from other vegetation types by the high mass ratio of tall trees (Bruelheide et al. 2018). Most of the available trait-based studies on forest herbs are restricted to specific biomes, such as temperate forests (Amatangelo et al. 2014; Sabatini et al. 2014; Kern et al. 2014; Vanneste et al. 2019; Campetella et al. 2020; Rolhauser et al. 2021; Kermavnar et al. 2021; Beck et al. 2022; Forey et al. 2023; Chianucci et al. 2024; Noualhaguet

et al. 2024; Chelli, Bricca, et al. 2024), and more such studies are needed from other biomes, forest types, and regions to test and refine theory directly and via meta-analysis. While studying herb traits, it is important to know that trait studies are limited by our understanding of plant-trait dimensionality, intraspecific variability, and trait relationships to abiotic gradients, fitness, and ecosystem function (Laughlin 2014; Shipley et al. 2016).

33. How do the functional traits of forest herbs vary within and among forest ecosystems and among successional forest stages?
34. What ecological information is captured by species identity versus functional traits versus phylogeny for herbaceous communities in forested ecosystems?
35. What is the relative importance of intra- versus interspecific trait variation along abiotic gradients?
36. How does the prevalence and magnitude of phenotypic plasticity in herbs compare to that in other plant growth forms?
37. What functional traits enable herbs to have high individual fitness and species diversity in forests where light is limited?
38. What are the relative effects of biotic and abiotic drivers on functional trait variation in herbs?
39. How do the cues, patterns, and mechanisms underlying phenology of leafing, flowering, and fruiting in herbs compare to those of trees, shrubs, epiphytes, and lianas?

3.8 | Demography and Population Dynamics

Herbaceous plants have been model systems for testing life-history theory and studying plant population dynamics (Harper 1980; Capdevila et al. 2022). However, much of this work has been focused on a limited suite of species and locations (Bierzychudek 1982; Whigham 2004; Vellend 2005; Bruna et al. 2009; Römer et al. 2024), in part because demographic work can be labor intensive and expensive (Queenborough et al. 2011). Expanding the taxonomic and geographic scope of demographic research will result in more robust and comprehensive life-history theory. For example, species in many tropical families (Zingiberaceae, Heliconiaceae, and Marantaceae) appear to have a shade-tolerant life history similar to that of tropical trees (Rundel et al. 1998; Takahashi 2004; Bruna and Ribeiro 2005a); if this is generally true of tropical species, it could lead to reconsider our view of a “typical” herb life-history strategy. It could also influence our broader understanding of forest dynamics: There is evidence that populations of these species rapidly expand following disturbance, potentially altering successional trajectories (George and Bazzaz 2014; Elliott et al. 2015) or maintaining forests in an alternate stable state (Pouteau et al. 2024).

40. How common is local adaptation in populations of herbaceous plant species in forests, and what drives variation in phenotypic plasticity among populations?

41. How do specific functional traits influence herb demography and population dynamics?
42. How do some forest herb species maintain high population sizes or growth rates in low-light conditions?
43. What is the relative importance of biotic and abiotic factors in driving the demographic vital rates and abundance of herbs?
44. How does sexual versus asexual reproduction influence the spatial genetic structure of forest herbs?
45. Does the magnitude of density dependence vary by life-history stage or life-history strategy?
46. What is the relationship in herbs between population size and population growth rate, and how does it compare to that of other plant groups?
47. How synchronous are the population dynamics among coexisting herb species over time and space?

3.9 | Ecosystem Ecology and Function

The impact of herbs on forest structure and function far exceeds their relative stature or biomass. Despite representing far less than 1% of forest aboveground biomass, the herbaceous layer can contribute up to 20% of foliar litter (Muller 2014); this litter has a far faster rate of decomposition than that of trees (Welch et al. 2007), making herbs central to carbon flux and nutrient cycling (Muller 2014; Neufield and Young 2014; Landuyt et al. 2019). This effect on nutrient cycles, coupled with empirical studies of herbs' role in ecosystem processes ranging from fire cycles to food-web assembly (Barton et al. 2009), suggests that the way in which they shape ecosystem function has been vastly underappreciated.

48. What ecosystem services do herbs provide? Which of those are uniquely provided by herbs, and what are the implications for ecosystem function of reductions in herb cover, biomass, or diversity?
49. What is the role and relative contribution of herbs to nutrient cycling in and across forests?
50. What are the direct and indirect pathways by which herbs influence forest carbon stocks?
51. How do parasitic and myco-heterotrophic herbs affect ecosystem processes in forests?

3.10 | Natural and Anthropogenic Disturbances

Given the physiology and ecology of forest herbs, it is perhaps not surprising that they appear particularly sensitive to natural and anthropogenic disturbances, including logging (Roberts 2004; Duguid and Ashton 2013; Duguid et al. 2013; Roberts and Gilliam 2014; Wyatt and Silman 2014), changes in flooding regime (Johnson and Waller 2013; Johnson et al. 2016), overabundance of herbivores (Mudrak et al. 2009; Waller 2014), and the historical legacies of agricultural practices (Bruna and Ribeiro 2005b; Flinn 2014). However, questions remain about

how herbs will respond to any synergistic effects of these disturbances with global-change phenomena, such as climate change (Bellemare and Moeller 2014) and nitrogen deposition (Gilliam 2014a), particularly in landscapes where their habitat has been lost or fragmented (Scott et al. 2022).

52. How do the frequency, intensity, and spatial extent of disturbances drive variation in herb community composition, structure, and function?
53. What persistent effects do past human activities (e.g., land use, management, and agriculture) have on the current diversity and distribution of herbs?
54. What is the relative role of vegetative reproduction, seed banks, and seed rain in the post-disturbance recovery and succession of forest herb and understory communities?
55. Do herb and tree communities respond similarly (in composition, structure, and/or function) to forest fragmentation and edge effects?
56. How do the diversity and dynamics of herbaceous plant communities differ among successional stages (e.g., old-growth and secondary forests)?
57. How does disturbance influence the population dynamics of herbs restricted to specific habitats or found primarily in old-growth forest?
58. What are the direct and indirect effects of canopy disturbances on herbaceous plants?
59. How do pollutants (e.g., atmospheric and chemical) alter herb communities, and are these responses consistent with those on other plant groups?
60. How do disturbances influence herb–animal interactions?
61. Does community composition or do particular traits serve as proxies for the capacity of herbs to adapt to disturbance?

3.11 | Forest Fire

Fire, both natural and anthropogenic, is a major disturbance in many forest ecosystems (McLauchlan et al. 2020) and a key driver of forest herb biodiversity. Natural fires allow for the ephemeral establishment of early successional herb species that would otherwise be excluded under forest canopies (Swanson et al. 2010; Hilmers et al. 2018; Spicer et al. 2022), whereas the heterogeneity of fire spread and intensity can promote diversity at broader spatial scales (Schoennagel et al. 2008; Meddens et al. 2018). Climate change is altering historical fire regimes and the frequency of severe, stand-replacing fires (Dennison et al. 2014; Higuera et al. 2021; McColl-Gausden et al. 2022), both of which could significantly impact herb dynamics or shift community composition in forests either directly or via associated environmental changes (Andrade et al. 2021; Coop et al. 2020; Guz et al. 2021; Gill et al. 2022; Rosenblad et al. 2023).

62. How does spatial and temporal variation in fire diversity influence the diversity, species composition, and

resiliency of herbaceous plant communities across fire-prone communities?

63. What are the consequences of alternative prescribed fire regimes on understory plant biodiversity and associated ecosystem functions?
64. What are the consequences of long-term fire suppression on the availability of herb species propagules in fire-adapted forests?
65. How will changing fire regimes impact herb populations and communities, especially in the less-studied forests in the Global South?

3.12 | Invasive Species

Forested ecosystems worldwide are impacted by the introduction of novel organisms, and are often stated as one of the largest risks to biodiversity (Mollot et al. 2017; Hald-Mortensen 2023) and introductions and their impacts are expected to continue to expand worldwide (Hulme 2009; Lovett et al. 2016). Currently, there is no universally accepted definition for invasive species, and the term is used across a wide variety of organisms, including mammals, plants, invertebrates, and microbes (Lockwood et al. 2013; Pereyra 2016; Iannone et al. 2020). Therefore, it is difficult to generalize the impacts of invasive species as a whole on forest herbs. For example, widespread outbreaks of forest pests or pathogens causing canopy death (e.g., emerald ash borer or chestnut blight in North America) will involve processes and impacts significantly different from that caused by mammals (e.g., beavers in Tierra del Fuego or feral pigs on Pacific islands; Pastur et al. 2006; Nogueira-Filho et al. 2009; Klooster et al. 2018; Karban and Karban 2024). Conversely, herbs have significant impacts as invasive species on forest ecosystems in many areas (Standish et al. 2001; Funk 2005; Wolfe et al. 2008; Wavrek et al. 2017).

66. What is the best way to quantify invasion and the impact of native and non-native species on herb communities?
67. How can we predict the risk of current and future invasion and impact by herbs in different forest ecosystems?
68. What are the ecological mechanisms by which invasive species (plants, animals, and microbes) alter herbaceous populations and communities in different forest biomes, and how do these change across spatial scales?

3.13 | Direct and Indirect Effects of Climate Change

Climate change is altering the demography, phenology, and distribution of forest herb species and their interactions with other species (Parmesan and Hanley 2015; Ash et al. 2017; Piao et al. 2019; Iler et al. 2021; Lee et al. 2022), but the generality and magnitude of these changes remain unclear. Addressing these lacunae requires a multifaceted approach integrating in situ observational studies, common garden and greenhouse experiments, simulations and modeling, and the analysis of community science datasets (Deng, Wei, et al. 2023).

69. How will climate change alter the community composition of forest herbs, and how do these changes compare with those predicted for woody plants?
70. How will the geographic distributions of forest herb species shift in response to predicted changes in climate?
71. How are the effects of climate change on forest herbs influenced by biotic and abiotic gradients?
72. What are the direct and indirect consequences of climate change for herb demography and population dynamics?
73. How will phenological mismatches with pollinators, dispersers, and herbivores affect spatio-temporal patterns of population and community dynamics?

3.14 | Cultural and Socioeconomical Value of Herbs

Although there have been monitoring, management, and development initiatives centered on socioeconomically important herbaceous species (Hongmao et al. 2002; Roberts 2002; Ticktin 2004; Buffa and Villani 2012; Mureithi et al. 2016; Chung et al. 2020), these efforts are rare, in large part due to the gaps in knowledge identified in the sections above.

74. What are the cultural, social, and economic values of forest herb species?
75. What are the ecological impacts of market-harvesting of socioeconomically important herbs for non-timber forest products (NTFPs)?

3.15 | Predicting Extinctions

Human activities are leading drivers of plant extinctions (Barnosky et al. 2011) and the widespread homogenization of plant communities (Daru et al. 2021). The risk and mechanisms of extinction faced by woody plant species have received widespread attention (Hubbell et al. 2008; Rivers et al. 2023; de Lima et al. 2024); the few studies addressing this topic with herbs point to both parallel responses and some important differences. For instance, herbs appear similarly susceptible to the loss of biotic interactions—especially pollination and seed dispersal (Wiegmann and Waller 2006). However, they may have the capacity to more quickly adapt to environmental change (Smith and Donoghue 2008; Smith and Beaulieu 2009), which may be why some studies suggest their overall risk of extinction could be lower than that of other plant groups (Leão et al. 2014; Chen et al. 2023).

76. What are the strongest predictors (e.g., phylogenetic attributes, functional traits, geographic range, and habitat) of local, regional, and global extinction risk for forest herbs?
77. How do the current extinction rates of forest herbs compare to those of woody plants, and what global-change phenomena are the primary drivers of herb extinction?
78. How does the extinction debt of herb species vary across forest types and groups of species?

3.16 | Direct Effects of Forest Management

Previous work has shown that tree removal, the use of herbicides, and other management practices applied to naturally regenerating forests influence the composition, functional diversity (Duguid and Ashton 2013; Duguid et al. 2013; Kusumoto et al. 2015; Peter and Harrington 2018; Stokely et al. 2022; McMichael et al. 2023), and community and population dynamics of forest herbs (de Grandpré and Bergeron 1997; Dovčiak and Halpern 2010; Royo et al. 2010; Elliott et al. 2011; Asbeck et al. 2021). However, many of these effects are often ecosystem- or site-specific, and it remains unclear what the consequences of these changes will be when combined with those of disturbance from past management, plant invasions (Oswalt et al. 2015; Huebner et al. 2018), or ongoing global change (Perring et al. 2018).

79. How do we assess whether management practices are meeting policy goals?
80. What are the major barriers to restoring forest herb populations, and what management techniques are needed to overcome these barriers?
81. What are the long-term effects of herbicides on the diversity and composition of native herb communities?
82. What are the relative effects of anthropogenic disturbances and management on trait diversity of herb communities?
83. What management practices are effective for controlling invasive herbaceous plants, and how does efficacy vary with forest type, geography, and species identity?
84. How can herbs be used to increase tree recruitment, regeneration, and performance, particularly in degraded ecosystems?
85. What are the effects of extracting timber or other resources on the abundance and population dynamics of forest herbs that are harvested as non-timber forest products?

3.17 | Indirect Effects of Management Practices and Land Use

Management for timber or other resources will have indirect effects on herbs, for example via direct impacts on the animals with which they interact. The same is true of management activities in the local or regional landscape matrices (Henry et al. 2020; Stewart and Byrne 2025). Previous studies have shown that the frequency and intensity of management practices can influence the population dynamics and demography of forest herbs (Royo et al. 2010; Elliott et al. 2011; Asbeck et al. 2021) and interact with species' traits, such as dispersal mechanism (Roberts 2004; Loehle et al. 2021). However, a complete understanding of the impact of forest management practices on herb communities is lacking.

86. How do management practices aimed at tree regeneration (e.g., site preparation and assisted regeneration) impact understory herb diversity and community dynamics?

87. How effective is retention harvesting at conserving understory herb species?
88. What is the impact of restoration practices on the colonization and establishment of native versus non-native herbs?
89. How do climate-adaptive silvicultural practices, including assisted migration, influence understory herb communities?
90. How does climate change influence the response of understory herb communities to forest management practices?
91. How do forest management practices influence herb–animal interactions?
92. How does forest management interact with thresholds of state transitions for understory herb communities?

3.18 | Conservation

Forest herbs rarely feature as an explicit target of conservation planning and reserve design, and even as the number of protected areas increases globally (Jones et al. 2018), these areas often do not overlap with the centers of diversity or distributions of important herb species (Joppa et al. 2013). Many herb species are subject to illegal harvesting for sale to collectors or for their putative medicinal properties, and are also impacted by other recreational activities in forests (van Andel and Havinga 2008; Wraith and Pickering 2017; Ticktin et al. 2018; Schmidt et al. 2019). Systematic efforts are needed to assess the abundance, distribution, and threats to herb species and to increase their representation in digitally accessible biodiversity databases used for conservation planning (e.g., the Global Biodiversity Information Facility; Feeley 2015; Trindade and Marques 2024). These efforts are also essential if herbs are to be included in international legal frameworks for conservation, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and other conservation systems, such as the one set by the International Union for Conservation of Nature (IUCN) (Brummitt et al. 2015).

93. How do current protected areas match the diversity and distribution of forest herbs?
94. What actions can be taken by the scientific community to identify herb species that should be the focus of conservation action and gather the required data for their inclusion in international conservation frameworks (e.g., CITES and IUCN)?

3.19 | Research Methods

This last suite of questions focuses on how we study herb communities. Workshop participants quickly honed in on the conspicuous lack of standard protocols for sampling herbs, even among researchers working in the same type of forest (Small and McCarthy 2002; Spicer et al. 2022). While recognizing not all studies for which herbs are used can use identical sampling methods, there was consensus among workshop participants

that the lack of systematic data collection hinders the ability to synthesize datasets, generalize across locations, or conduct meta-analyses (McCarthy 2014).

95. What are the most effective methods to sample herb diversity to allow for cross-site comparisons across different forest types?
96. How can we efficiently track the changes and variation in the abundance of species, especially those that are rare or ephemeral?
97. Can we synthesize data collected to date and use the lessons learned to develop standard protocols for future surveys and studies?
98. How does collector bias influence our understanding of plant biodiversity in forest ecosystems?
99. Given the taxonomic challenges in identifying many herb species, what is the best approach for standardizing and comparing diversity at different taxonomic levels?
100. How can we use emerging technologies (e.g., remote sensing, LiDAR, and hyperspectral imagery) to characterize the structure and composition of understory herb communities at multiple scales?

4 | Discussion

The 100 questions above address important gaps in our understanding of a globally widespread, species-rich, biologically complex, and ecologically critical group of plants. In addition to identifying promising areas of research for specific subdisciplines, the questions and the workshop discussions surrounding them also suggest four overarching themes and challenges faced by scientists studying forest herbs.

4.1 | Theme 1: Defining “Herbaceous Plants”

One would expect a commonly used term as “herb” to have a clear physiognomic, morphological, or anatomical definition. Although the presence of soft, non-woody stems is their historically consistent and defining characteristic, more specific definitions have been offered based on anatomy (Eiten 1991; Carlquist 2009) and other characteristics (Anon 2025). A temperate forest perspective of such definitions can be observed in ecological studies of the “herbaceous layer”: undergrowth defined by plants of low stature that frequently grow in dense mats of intermingling species (Gilliam 2014b). The workshop participants did not attempt to fine-tune any existing terrestrial, non-woody plants as herbs, that is, any plant without angiosperm- or gymnosperm-wood above the ground, and/or without highly lignified stems. Hence, ferns, flowering plants, and non-flowering plants with non-woody stems that grow on the forest floor were considered terrestrial herbs, whereas lignified monocots such as palms and bamboos were not considered. Other prominent non-woody plant life forms not rooted (e.g., epiphytes and hemi-epiphytes) or fully established (e.g., secondary hemi-epiphytes) on the forest floor were excluded from the definition. This challenge in defining herbs, both botanically and ecologically, has

important implications for how these plants are studied and for drawing general conclusions about “herbaceous plants” that transcend forest types and biomes. That said, it is important for studies to make clear how the term “herb” is being defined and applied, and especially the distinction between herbs and the herb, understory, or ground “layer,” if the “layer” also contains woody seedlings, saplings, or shrubs.

4.2 | Theme 2: Research Methods

Studying a group with such marked variation in life form, life-history strategy, and clonality poses myriad methodological challenges (Zobel and Liira 1997; Small and McCarthy 2002; Spicer et al. 2022). These issues have resulted in researchers taking varied and often idiosyncratic approaches to data collection (Zobel and Liira 1997; Burton et al. 2011; Queenborough et al. 2011), resulting in data that are often incomparable across different studies, forest types, and biomes. There are existing protocols followed in certain temperate forests (Peet et al. 1998, 2012, 2018), but these need to be modified and standardized to include other biomes and create globally comparable datasets. A few regional herb databases (e.g., Amazonia’s HERBase) highlight progress in data compilation and echo challenges in methodological standardization (André et al. 2023). Addressing this methodological diversity by developing standardized census protocols was viewed by workshop attendees as a major priority. The power of internationally standardized protocols is evident from the 1000+ papers resulting from global tree plot networks, such as ForestGEO (Davies et al. 2021) and Rainfor (Malhi et al. 2002; Peacock et al. 2007). More recently, efforts to standardize protocols for lianas (Schnitzer et al. 2015) and arboreal epiphytes (Nieder et al. 1999; Freiberg and Freiberg 2000; Köster et al. 2009; Adhikari et al. 2021; Taylor et al. 2022; Krömer et al. 2025) have further advanced theory (DeWalt et al. 2015; Verbeeck et al. 2024) and conservation practice (Campbell et al. 2015). Our vision is of a similar standardized sampling protocol integrated into existing forest dynamics plots that outlines baseline data to be collected to enable cross-site comparisons of herbaceous plant communities in forests around the world.

4.3 | Theme 3: Cross-System Comparisons

The overwhelming focus on trees as systems with which to test ecological theory is leading to questions as to how representative this life form is of all plants (Radhamoni et al. 2023, 2025). Many of the questions identified by participants—including those on the drivers of species distributions, mechanisms of coexistence, and responses to habitat fragmentation, climate change, and other anthropogenic impacts—emerged as explicit comparisons between trees and herbs (Radhamoni et al. 2025). In contrast, other questions were centered exclusively on herbs, with the primary interest being the potential for generality across forest types (e.g., dry vs. moist forest), biomes (tropical vs. temperate), or anthropogenic impacts (e.g., fragmented vs. continuous forest). The herbaceous communities of many forests and forest types across the Earth remain understudied, especially in the tropics and Global South. Expanding cross-system comparisons was viewed as a priority by workshop participants.

4.4 | Theme 4: Taxonomy, Systematics, and Evolutionary Studies

Taxonomy and systematics face a number of well-known and multifaceted challenges that impede our ability to describe and conserve global biodiversity (Meyer et al. 2016; Engel et al. 2021). As these challenges are particularly pressing in the tropics and extra-temperate forests of the Global South (Rao 2012; Goodwin et al. 2015; Shennan-Farpón et al. 2021), researchers studying tropical herbs are often faced with low taxonomic resolution for even prominent groups, a dearth of flora or field guides, limited resources for maintaining collections, a backlog of specimens to be identified, and declining numbers of both taxonomic authorities and field technicians with botanical expertise (Goodwin et al. 2015; Crisci et al. 2020; Stroud et al. 2022; Luján et al. 2024). Therefore, it is likely that many surveys conducted in the tropics and Global South underestimate the true diversity in any given location. Along with the need for standardized census protocols mentioned above, increased attention and funding for studies of herbaceous plant species in tropical forests are critical for filling this gap in our understanding of global plant diversity. The use of emerging technologies (e.g., AI for species identification) and community engagement (e.g., iNaturalist, Wolf et al. 2022; Yancy et al. 2024) also hold great promise for improving efforts to identify and study forest herbs.

5 | Conclusion

Herbs comprise a major proportion of the plant diversity in the world's forests, where they serve as habitat and food for myriad animal taxa and provide economically and culturally vital NTFPs. Despite being tractable systems readily amenable to experimental manipulation, herbs remain underused as model systems for testing ecological theory, in part because several aspects of their biology make it challenging to compare and synthesize the results of studies conducted with disparate methods or in different forest types. Similarly, geographic biases in research attention mean that the long-term and extensive data from north temperate forests may also be unrepresentative. The 100 questions posed here can serve as a guide for generating high-priority information about the ecology of this fundamentally important group in less-studied forests, as well as for advancing our broader understanding of ecological theory and the response of biodiversity to ongoing and emergent threats.

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Acknowledgements

We thank all respondents who provided input through our open community survey.

Funding

This material is based upon work supported by the US National Science Foundation under grant no. 2203958, and partly by grant nos. 2220980 and 1907190. We thank the Oak Spring Garden Foundation for hosting participants during the forest herb workshop.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the [Supporting Information](#) of this article.

References

- Adhikari, Y. P., S. Hoffmann, R. M. Kunwar, M. Bobrowski, A. Jentsch, and C. Beierkuhnlein. 2021. "Vascular Epiphyte Diversity and Host Tree Architecture in Two Forest Management Types in the Himalaya." *Global Ecology and Conservation* 27: e01544. <https://doi.org/10.1016/j.gecco.2021.e01544>.
- Albornoz, F. E., S. M. Prober, M. H. Ryan, and R. J. Standish. 2022. "Ecological Interactions Among Microbial Functional Guilds in the

- Plant-Soil System and Implications for Ecosystem Function." *Plant and Soil* 476: 301–313. <https://doi.org/10.1007/s11004-022-05479-1>.
- Amatangelo, K. L., S. E. Johnson, D. A. Rogers, and D. M. Waller. 2014. "Trait–Environment Relationships Remain Strong Despite 50 Years of Trait Compositional Change in Temperate Forests." *Ecology* 95: 1780–1791. <https://doi.org/10.1890/13-0757.1>.
- Andrade, A. J., D. F. Tomback, T. R. Seastedt, and S. Mellmann-Brown. 2021. "Soil Moisture Regime and Canopy Closure Structure Subalpine Understory Development During the First Three Decades Following Fire." *Forest Ecology and Management* 483: 118783. <https://doi.org/10.1016/j.foreco.2020.118783>.
- André, T., G. M. Moulatlet, T. E. Almeida, et al. 2023. "HERBase: A Collection of Understorey Herb Vegetation Plots From Amazonia." *Acta Amazonica* 53: 114–121. <https://doi.org/10.1590/1809-4392202023150>.
- Anon. 2025. "A Grammatical Dictionary of Botanical Latin." <https://www.mobot.org/mobot/latindict/keyDetail.aspx?keyWord=herb>.
- Asbeck, T., F. Sabatini, A. L. D. Augustynczyk, et al. 2021. "Biodiversity Response to Forest Management Intensity, Carbon Stocks and Net Primary Production in Temperate Montane Forests." *Scientific Reports* 11: 1625. <https://doi.org/10.1038/s41598-020-80499-4>.
- Ash, J. D., T. J. Givnish, and D. M. Waller. 2017. "Tracking Lags in Historical Plant Species' Shifts in Relation to Regional Climate Change." *Global Change Biology* 23: 1305–1315. <https://doi.org/10.1111/gcb.13429>.
- Barabás, G., R. D'Andrea, and S. M. Stump. 2018. "Chesson's Coexistence Theory." *Ecological Monographs* 88: 277–303. <https://www.jstor.org/stable/26998022>.
- Barnosky, A. D., N. Matzke, S. Tomiya, et al. 2011. "Has the Earth's Sixth Mass Extinction Already Arrived?" *Nature* 471: 51–57. <https://doi.org/10.1038/nature09678>.
- Barrett, S. C. H., and K. Helenurm. 1987. "The Reproductive Biology of Boreal Forest Herbs. I. Breeding Systems and Pollination." *Canadian Journal of Botany* 65: 2036–2046. <https://doi.org/10.1139/b87-278>.
- Barry, K. E., and S. A. Schnitzer. 2021. "Are We Missing the Forest for the Trees? Conspecific Negative Density Dependence in a Temperate Deciduous Forest." *PLoS One* 16: e0245639. <https://doi.org/10.1371/journal.pone.0245639>.
- Bartels, S. F., and H. Y. H. Chen. 2012. "Mechanisms Regulating Epiphytic Plant Diversity." *Critical Reviews in Plant Sciences* 31: 391–400. <https://doi.org/10.1080/07352689.2012.680349>.
- Barton, B. T., A. P. Beckerman, and O. J. Schmitz. 2009. "Climate Warming Strengthens Indirect Interactions in an Old-Field Food Web." *Ecology* 90: 2346–2351. <https://doi.org/10.1890/08-2254.1>.
- Beck, J. J. 2021. "Variation in Plant–Soil Interactions Among Temperate Forest Herbs." *Plant Ecology* 222: 1225–1238. <https://doi.org/10.1007/s11258-021-01173-x>.
- Beck, J. J., and T. J. Givnish. 2021. "Fine-Scale Environmental Heterogeneity and Spatial Niche Partitioning Among Spring-Flowering Forest Herbs." *American Journal of Botany* 108: 63–73. <https://doi.org/10.1002/ajb2.1593>.
- Beck, J. J., D. Li, S. E. Johnson, et al. 2022. "Functional Traits Mediate Individualistic Species–Environment Distributions at Broad Spatial Scales While Fine-Scale Species Associations Remain Unpredictable." *American Journal of Botany* 109: 1991–2005. <https://doi.org/10.1002/ajb2.16085>.
- Bellemare, J., and D. A. Moeller. 2014. "Climate Change and Forest Herbs of Temperate Deciduous Forests." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 460–493. Oxford University Press. <https://doi.org/10.1093/acprof:osobl/9780199837656.003.0021>.
- Berger, A. L., and K. J. Puettmann. 2000. "Overstory Composition and Stand Structure Influence Herbaceous Plant Diversity in the Mixed Aspen Forest of Northern Minnesota." *American Midland Naturalist* 143: 111–125. [https://doi.org/10.1674/0003-0031\(2000\)143\[0111:OCASSI\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2000)143[0111:OCASSI]2.0.CO;2).
- Bierzchudek, P. 1982. "Life Histories and Demography of Shade-Tolerant Temperate Forest Herbs: A Review." *New Phytologist* 90: 757–776. <https://doi.org/10.1111/j.1469-8137.1982.tb03285.x>.
- Blyth, L. H., L. J. Ouborg, D. M. Johnson, and L. J. Anderson. 2013. "The Short-Term Germination and Establishment Success of Deer-Dispersed Seeds in Mesic Temperate Forests." *Journal of the Torrey Botanical Society* 140: 334–348. <https://doi.org/10.3159/TORREY-D-13-00006.1>.
- Boulanger, V., J.-L. Dupouey, F. Archaux, et al. 2018. "Ungulates Increase Forest Plant Species Richness to the Benefit of Non-Forest Specialists." *Global Change Biology* 24: e485–e495. <https://doi.org/10.1111/gcb.13899>.
- Bratton, S. P. 1976. "Resource Division in an Understory Herb Community: Responses to Temporal and Microtopographic Gradients." *American Naturalist* 110: 679–693. <https://doi.org/10.1086/283097>.
- Bruehlheide, H., J. Dengler, O. Purschke, et al. 2018. "Global Trait–Environment Relationships of Plant Communities." *Nature Ecology & Evolution* 2: 1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>.
- Brummitt, N. A., S. P. Bachman, J. Griffiths-Lee, et al. 2015. "Green Plants in the Red: A Baseline Global Assessment for the IUCN Sampled Red List Index for Plants." *PLoS One* 10: e0135152. <https://doi.org/10.1371/journal.pone.0135152>.
- Bruna, E. M., I. J. Fiske, and M. D. Trager. 2009. "Habitat Fragmentation and Plant Populations: Is What We Know Demographically Irrelevant?" *Journal of Vegetation Science* 20: 569–576. <https://doi.org/10.1111/j.1654-1103.2009.01060.x>.
- Bruna, E. M., and M. B. N. Ribeiro. 2005a. "The Compensatory Responses of an Understory Herb to Experimental Damage Are Habitat-Dependent." *American Journal of Botany* 92: 2101–2106.
- Bruna, E. M., and M. B. N. Ribeiro. 2005b. "Regeneration and Population Structure of *Heliconia acuminata* in Amazonian Secondary Forests With Contrasting Land-Use Histories." *Journal of Tropical Ecology* 21: 127–131. <https://doi.org/10.3732/ajb.92.12.2101>.
- Buffa, G., and M. Villani. 2012. "Are the Ancient Forests of the Eastern Po Plain Large Enough for a Long Term Conservation of Herbaceous Nemoral Species?" *Plant Biosystems* 146: 970–984. <https://doi.org/10.1080/11263504.2012.704887>.
- Bugno-Pogoda, A., R. Durak, and T. Durak. 2021. "Impact of Forest Management on the Temporal Dynamics of Herbaceous Plant Diversity in the Carpathian Beech Forests Over 40 Years." *Biology* 10: 406. <https://doi.org/10.3390/biology10050406>.
- Burton, J. I., D. J. Mladenoff, M. K. Clayton, and J. A. Forrester. 2011. "The Roles of Environmental Filtering and Colonization in the Fine-Scale Spatial Patterning of Ground-Layer Plant Communities in North Temperate Deciduous Forests." *Journal of Ecology* 99: 764–776. <https://doi.org/10.1111/j.1365-2745.2011.01807.x>.
- Burton, J. I., S. S. Perakis, J. R. Brooks, and K. J. Puettmann. 2020. "Trait Integration and Functional Differentiation Among Co-Existing Plant Species." *American Journal of Botany* 107: 628–638. <https://doi.org/10.1002/ajb2.1451>.
- Burton, J. I., S. S. Perakis, S. C. McKenzie, C. E. Lawrence, and K. J. Puettmann. 2017. "Intraspecific Variability and Reaction Norms of Forest Understorey Plant Species Traits." *Functional Ecology* 31: 1881–1893. <https://doi.org/10.1111/1365-2435.12898>.
- Campbell, M. J., W. Edwards, E. Odell, D. Mohandass, and W. F. Laurance. 2015. "Can Lianas Assist in Rainforest Restoration?" *Tropical Conservation Science* 8: 257–273. <https://doi.org/10.1177/194008291500800119>.

- Campetella, G., S. Chelli, E. Simonetti, et al. 2020. "Plant Functional Traits Are Correlated With Species Persistence in the Herb Layer of Old-Growth Beech Forests." *Scientific Reports* 10: 19253. <https://doi.org/10.1038/s41598-020-76289-7>.
- Capdevila, P., I. Stott, J. Cant, et al. 2022. "Life History Mediates the Trade-Offs Among Different Components of Demographic Resilience." *Ecology Letters* 25: 1566–1579. <https://doi.org/10.1111/ele.14004>.
- Carlquist, S. 2009. "Xylem Heterochrony: An Unappreciated Key to Angiosperm Origin and Diversifications." *Botanical Journal of the Linnean Society* 161: 26–65. <https://doi.org/10.1111/j.1095-8339.2009.00991.x>.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. "Towards a Worldwide Wood Economics Spectrum." *Ecology Letters* 12: 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
- Chazdon, R. L., P. H. S. Brancalion, L. Laestadius, et al. 2016. "When Is a Forest a Forest? Forest Concepts and Definitions in the Era of Forest and Landscape Restoration." *Ambio* 45: 538–550. <https://doi.org/10.1007/s13280-016-0772-y>.
- Chelli, S., A. Bricca, J. L. Tsakalos, et al. 2024. "Multiple Drivers of Functional Diversity in Temperate Forest Understories: Climate, Soil, and Forest Structure Effects." *Science of the Total Environment* 916: 170258. <https://doi.org/10.1016/j.scitotenv.2024.170258>.
- Chelli, S., J. Klimešová, J. L. Tsakalos, and G. Puglielli. 2024. "Unravelling the Clonal Trait Space: Beyond Above-Ground and Fine-Root Traits." *Journal of Ecology* 112: 730–740. <https://doi.org/10.1111/1365-2745.14265>.
- Chen, K., L. Hu, C. Wang, W. Yang, H. Zi, and L. Manuel. 2021. "Herbaceous Plants Influence Bacterial Communities, While Shrubs Influence Fungal Communities in Subalpine Coniferous Forests." *Forest Ecology and Management* 500: 119656. <https://doi.org/10.1016/j.foreco.2021.119656>.
- Chen, T. V., T. Boonma, and N. T. T. Hien. 2025. "An Overview of the Chemical Compositions and Biological Activities of Essential Oils From Selected *Zingiber* Species (Zingiberaceae)." *Natural Product Communications* 20: 1934578X251329422. <https://doi.org/10.1177/1934578X251329422>.
- Chen, Y., Y. Li, L. Wang, et al. 2024. "Heterogeneity of Leaf Stoichiometry of Different Life Forms Along Environmental Transects in Typical Ecologically Fragile Areas of China." *Science of the Total Environment* 910: 168495. <https://doi.org/10.1016/j.scitotenv.2023.168495>.
- Chen, Y., Y. Wu, Y. Dong, et al. 2023. "Extinction Risk of Chinese Angiosperms Varies Between Woody and Herbaceous Species." *Diversity and Distributions* 29: 232–243. <https://doi.org/10.1111/ddi.13655>.
- Chianucci, F., F. Napoleone, C. Ricotta, et al. 2024. "Silvicultural Regime Shapes Understory Functional Structure in European Forests." *Journal of Applied Ecology* 61: 2350–2364. <https://doi.org/10.1111/1365-2664.14740>.
- Christopher, C. C., S. F. Matter, and G. N. Cameron. 2014. "Individual and Interactive Effects of Amur Honeysuckle (*Lonicera maackii*) and White-Tailed Deer (*Odocoileus virginianus*) on Herbs in a Deciduous Forest in the Eastern United States." *Biological Invasions* 16: 2247–2261. <https://doi.org/10.1007/s10530-014-0661-x>.
- Chung, M. Y., S. Son, S. Herrando-Moraira, et al. 2020. "Incorporating Differences Between Genetic Diversity of Trees and Herbaceous Plants in Conservation Strategies." *Conservation Biology* 34: 1142–1151. <https://doi.org/10.1111/cobi.13467>.
- Churchland, C., and S. J. Grayston. 2014. "Specificity of Plant-Microbe Interactions in the Tree Mycorrhizosphere Biome and Consequences for Soil C Cycling." *Frontiers in Microbiology* 5: 261. <https://doi.org/10.3389/fmicb.2014.00261>.
- Cicuzza, D., T. Krömer, A. D. Poulsen, et al. 2013. "A Transcontinental Comparison of the Diversity and Composition of Tropical Forest Understory Herb Assemblages." *Biodiversity and Conservation* 22: 755–772. <https://doi.org/10.1007/s10531-013-0447-y>.
- Cooke, S. J., J. N. Bergman, C. L. Madliger, et al. 2021. "One Hundred Research Questions in Conservation Physiology for Generating Actionable Evidence to Inform Conservation Policy and Practice." *Physiology* 9: coab009. <https://doi.org/10.1093/conphys/coab009>.
- Coomes, D. A., R. B. Allen, W. A. Bentley, et al. 2005. "The Hare, the Tortoise and the Crocodile: The Ecology of Angiosperm Dominance, Conifer Persistence and Fern Filtering." *Journal of Ecology* 93: 918–935. <https://doi.org/10.1111/j.1365-2745.2005.01012.x>.
- Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *Bioscience* 70: 659–673. <https://doi.org/10.1093/biosci/biaa061>.
- Costa, F. R. C. 2004. "Structure and Composition of the Ground-Herb Community in a Terra-Firme Central Amazonian Forest." *Acta Amazonica* 34: 53–59. <https://doi.org/10.1590/S0044-59672004000100007>.
- Costa, F. R. C. 2006. "Mesoscale Gradients of Herb Richness and Abundance in Central Amazonia." *Biotropica* 38: 711–717. <https://doi.org/10.1111/j.1744-7429.2006.00211.x>.
- Crisci, J. V., L. Katinas, M. J. Apodaca, and P. C. Hoch. 2020. "The End of Botany." *Trends in Plant Science* 25: 1173–1176. <https://doi.org/10.1016/j.tplants.2020.09.012>.
- Curtis, J. T. 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press.
- da Silva Fortirer, J., A. Grandis, D. Pagliuso, C. de Toledo Castanho, and M. S. Buckeridge. 2023. "Meta-Analysis of the Responses of Tree and Herb to Elevated CO₂ in Brazil." *Scientific Reports* 13: 15832. <https://doi.org/10.1038/s41598-023-40783-5>.
- Daru, B. H., T. J. Davies, C. G. Willis, et al. 2021. "Widespread Homogenization of Plant Communities in the Anthropocene." *Nature Communications* 12: 6983. <https://doi.org/10.1038/s41467-021-27186-8>.
- Dattaraja, H. S., S. Pulla, H. S. Suresh, M. S. Nagaraja, C. A. Srinivasa Murthy, and R. Sukumar. 2018. "Woody Plant Diversity in Relation to Environmental Factors in a Seasonally Dry Tropical Forest Landscape." *Journal of Vegetation Science* 29: 704–714. <https://doi.org/10.1111/jvs.12652>.
- Davies, S. J., I. Abiem, K. Abu Salim, et al. 2021. "ForestGEO: Understanding Forest Diversity and Dynamics Through a Global Observatory Network." *Biological Conservation* 253: 108907. <https://doi.org/10.1016/j.biocon.2020.108907>.
- de Grandpré, L., and Y. Bergeron. 1997. "Diversity and Stability of Understorey Communities Following Disturbance in the Southern Boreal Forest." *Journal of Ecology* 85: 777–784. <https://doi.org/10.2307/2960601>.
- de Lima, R. A. F., G. Dauby, A. L. de Gasper, et al. 2024. "Comprehensive Conservation Assessments Reveal High Extinction Risks Across Atlantic Forest Trees." *Science* 383: 219–225. <https://doi.org/10.1126/science.abq5099>.
- Deng, J., S. Fang, X. Fang, et al. 2023. "Forest Understory Vegetation Study: Current Status and Future Trends." *Forest Research* 14: 3–6. <https://doi.org/10.48130/FR-2023-0006>.
- Deng, T., Q. Du, Y. Zhu, and S. A. Queenborough. 2025. "Environmental Drivers of Herbaceous Plant Diversity in the Understory Community of a Warm-Temperate Forest." *Plant Diversity* 47: 282–290.
- Deng, T., Y. Wei, S. Ren, and Y. Zhu. 2023. "Effects of Topography and Stand Structure of Warm Temperate Deciduous Broad-Leaved Forest

- on Understory Herb Diversity in Donglingshan." *Beijing. Biodiversity Science* 31: 22671. <https://doi.org/10.1016/j.pld.2025.01.003>.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. "Large Wildfire Trends in the Western United States, 1984–2011." *Geophysical Research Letters* 41: 2928–2933. <https://doi.org/10.1002/2014GL059576>.
- DeWalt, S. J., S. A. Schnitzer, L. F. Alves, et al. 2015. "Biogeographical Patterns of Liana Abundance and Diversity." In *Ecology of Lianas*, edited by S. A. Schnitzer, F. B. Burnham, and F. E. Putz, 131–146. John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118392409.ch11>.
- Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. "The Global Spectrum of Plant Form and Function." *Nature* 529: 167–171.
- Dovčiak, M., and C. B. Halpern. 2010. "Positive Diversity-Stability Relationships in Forest Herb Populations During Four Decades of Community Assembly." *Ecology Letters* 13: 1300–1309. <https://doi.org/10.1038/nature16489>.
- Duguid, M. C., and M. S. Ashton. 2013. "A Meta-Analysis of the Effect of Forest Management for Timber on Understory Plant Species Diversity in Temperate Forests." *Forest Ecology and Management* 303: 81–90. <https://doi.org/10.1016/j.foreco.2013.04.009>.
- Duguid, M. C., B. R. Frey, D. S. Ellum, M. Kelty, and M. S. Ashton. 2013. "The Influence of Ground Disturbance and Gap Position on Understory Plant Diversity in Upland Forests of Southern New England." *Forest Ecology and Management* 303: 148–159. <https://doi.org/10.1016/j.foreco.2013.04.018>.
- Eiten, G. 1991. "What Is a Herb? (With Examples From the Tropical 'Savanna' of Brazil and the Humid Temperate Zone of Poland)." *Veröffentlichungen Des Geobotanischen Institutes, Stiftung Rübél* 106: 288–304.
- Ellenberg, H. 1988. *Vegetation Ecology of Central Europe*. 4th ed. Cambridge University Press.
- Elliott, K. J., C. A. Harper, and B. Collins. 2011. "Herbaceous Response to Type and Severity of Disturbance." In *Sustaining Young Forest Communities*, edited by C. Greenberg, B. Collins, and F. Thompson Iii, 97–119. Springer. https://doi.org/10.1007/978-94-007-1620-9_7.
- Elliott, K. J., J. M. Vose, J. D. Knoepp, B. D. Clinton, and B. D. Kloeppel. 2015. "Functional Role of the Herbaceous Layer in Eastern Deciduous Forest Ecosystems." *Ecosystems* 18: 221–236. <https://doi.org/10.1007/s10021-014-9825-x>.
- Ellstrand, N. C., R. Whitkus, and L. H. Rieseberg. 1996. "Distribution of Spontaneous Plant Hybrids." *Proceedings of the National Academy of Sciences of the United States of America* 93: 5090–5093. <https://doi.org/10.1073/pnas.93.10.5090>.
- Engel, M. S., L. M. P. Ceriaco, G. M. Daniel, et al. 2021. "The Taxonomic Impediment: A Shortage of Taxonomists, Not the Lack of Technical Approaches." *Zoological Journal of the Linnean Society* 193: 381–387. <https://doi.org/10.1093/zoolinlean/zlab072>.
- Esquivel-Muelbert, A., T. R. Baker, K. G. Dexter, et al. 2017. "Seasonal Drought Limits Tree Species Across the Neotropics." *Ecography* 40: 618–629. <https://doi.org/10.1111/ecog.01904>.
- Faison, E. K., D. R. Foster, and S. DeStefano. 2017. "Long-Term Deer Exclusion Has Complex Effects on a Suburban Forest Understory." *Rhodora* 118: 382–402. <https://doi.org/10.3119/15-35>.
- Feeley, K. 2015. "Are We Filling the Data Void? An Assessment of the Amount and Extent of Plant Collection Records and Census Data Available for Tropical South America." *PLoS One* 10: e0125629. <https://doi.org/10.1371/journal.pone.0125629>.
- Fernandes, G. W., O. Varela, E. H. Bucher, et al. 2002. "Gall-Forming Insects on Woody and Herbaceous Plant Species of the Semi-Arid Chaco Forest, Argentina." *Lundiana: International Journal of Biodiversity* 3: 61–66.
- Filgueiras, T. S. 2002. "7. Herbaceous plant communities." In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, edited by P. S. Oliveira and R. J. Marquis, 121–139. Columbia University Press.
- Fine, P. V. A. 2015. "Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity." *Annual Review of Ecology, Evolution, and Systematics* 46: 369–392. <https://doi.org/10.1146/annurev-ecolsys-112414-054102>.
- Flinn, K. M. 2014. "Agricultural Legacies in Forest Herb Communities." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 438–444. Oxford University Press.
- Forey, E., S. Y. F. Lodhar, S. D. Galvin, et al. 2023. "Alien Palm Invasion Leads to Selective Biotic Filtering of Resident Plant Communities Towards Competitive Functional Traits." *Biological Invasions* 25: 1489–1508. <https://doi.org/10.1007/s10530-022-02991-4>.
- Freiberg, M., and E. Freiberg. 2000. "Epiphyte Diversity and Biomass in the Canopy of Lowland and Montane Forests in Ecuador." *Journal of Tropical Ecology* 16: 673–688. <https://doi.org/10.1017/S026646740001644>.
- Fukami, T. 2015. "Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects." *Annual Review of Ecology, Evolution, and Systematics* 46: 1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>.
- Funk, J. L. 2005. "*Hedydium gardnerianum* Invasion Into Hawaiian Montane Rainforest: Interactions Among Litter Quality, Decomposition Rate, and Soil Nitrogen Availability." *Biogeochemistry* 76, no. 3: 441–451. <https://doi.org/10.1007/s10533-005-7657-7>.
- Gandhi, K. J. K., and D. A. Herms. 2010. "Direct and Indirect Effects of Alien Insect Herbivores on Ecological Processes and Interactions in Forests of Eastern North America." *Biological Invasions* 12: 389–405. <https://doi.org/10.1007/s10530-009-9627-9>.
- Geng, Q., M. Arif, F. Yin, et al. 2024. "Characteristics of Forest Understory Herbaceous Vegetation and Its Influencing Factors in Biodiversity Hotspots in China." *Ecological Indicators* 167: 112634. <https://doi.org/10.1016/j.ecolind.2024.112634>.
- Gentry, A. H., and C. Dodson. 1987. "Contribution of Nontrees to Species Richness of a Tropical Rain Forest." *Biotropica* 19: 149–156. <https://www.jstor.org/stable/2388737>.
- Gentry, A. H., and L. H. Emmons. 1987. "Geographical Variation in Fertility, Phenology, and Composition of the Understory of Neotropical Forests." *Biotropica* 19: 216–227. <https://www.jstor.org/stable/2388339>.
- George, L. O., and F. A. Bazzaz. 1999. "The Fern Understory as an Ecological Filter: Growth and Survival of Canopy-Tree Seedlings." *Ecology* 80, no. 3: 846–856. [https://doi.org/10.1890/0012-9658\(1999\)080\[0846:TFUAAE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0846:TFUAAE]2.0.CO;2).
- George, L. O., and F. A. Bazzaz. 2014. "The Herbaceous Layer as a Filter Determining Spatial Pattern in Forest Tree Regeneration." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. S. Gilliam, First ed., 340–355. Oxford University Press.
- Gilbert, B., and M. J. Lechowicz. 2004. "Neutrality, Niches, and Dispersal in a Temperate Forest Understory." *Proceedings of the National Academy of Sciences* 101: 7651–7656. <https://doi.org/10.1073/pnas.0400814101>.
- Gill, N. S., M. G. Turner, C. D. Brown, et al. 2022. "Limitations to Propagule Dispersal Will Constrain Postfire Recovery of Plants and Fungi in Western Coniferous Forests." *Bioscience* 72: 347–364. <https://doi.org/10.1093/biosci/biab139>.
- Gilliam, F. S. 2007. "The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems." *Bioscience* 57: 845. <https://doi.org/10.1641/B571007>.
- Gilliam, F. S. 2014a. "Introduction: The Herbaceous Layer—The Forest Between the Trees." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. S. Gilliam, Second ed., xvi–9. Oxford University Press.

- Gilliam, F. S. 2014b. "Effects of Excess Nitrogen Deposition on the Herbaceous Layer of Eastern North American Forests." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 445–459. Oxford University Press.
- Goodwin, Z. A., D. J. Harris, D. Filer, J. R. I. Wood, and R. W. Scotland. 2015. "Widespread Mistaken Identity in Tropical Plant Collections." *Current Biology* 25: R1066–R1067. <https://doi.org/10.1016/j.cub.2015.10.002>.
- Grime, J. P. 2006. "Trait Convergence and Trait Divergence in Herbaceous Plant Communities: Mechanisms and Consequences." *Journal of Vegetation Science* 17: 255–260. <https://doi.org/10.1111/j.1654-1103.2006.tb02444.x>.
- Guiden, P. W. 2017. "Spatial Heterogeneity in White-Tailed Deer Activity Increases Seed Dispersal of Shade-Intolerant Plants Near Forest Edges in Fragmented Forests." *Journal of the Torrey Botanical Society* 144: 371–378. <https://doi.org/10.3159/TORREY-D-16-00045.1>.
- Guz, J., N. S. Gill, and D. Kulakowski. 2021. "Long-Term Empirical Evidence Shows Post-Disturbance Climate Controls Post-Fire Regeneration." *Journal of Ecology* 109: 4007–4024. <https://doi.org/10.1111/1365-2745.13771>.
- Hald-Mortensen, C. 2023. "The Main Drivers of Biodiversity Loss: A Brief Overview." *Journal of Ecology and Natural Resources* 7: 000346. <https://doi.org/10.2139/ssrn.4539049>.
- Hames, R., and I. Hames. 1976. *Ye'kwana Basketry: Its Cultural Context*. Faculty Publications.
- Harper, J. L. 1980. "Plant Demography and Ecological Theory." *Oikos* 35: 244–253. <https://www.jstor.org/stable/3544432>.
- Haukioja, E., and J. Koricheva. 2000. "Tolerance to Herbivory in Woody vs. Herbaceous Plants." *Evolutionary Ecology* 14: 551–562. <https://doi.org/10.1023/A:1011091606022>.
- Havrdová, A., J. Douda, K. Boublik, et al. 2025. "Decadal Decline in Herbaceous Species Richness in Wetland Forests: Effects of an Introduced Pathogen and Environmental Change." *Forest Ecology and Management* 583: 122569. <https://doi.org/10.1016/j.foreco.2025.122569>.
- Henry, E. H., M. O. Burford Reiskind, A. D. Land, and N. M. Haddad. 2020. "Maintaining Historic Disturbance Regimes Increases Species' Resilience to Catastrophic Hurricanes." *Global Change Biology* 26: 798–806. <https://doi.org/10.1111/gcb.14932>.
- Higuera, P. E., B. N. Shuman, and K. D. Wolf. 2021. "Rocky Mountain Subalpine Forests Now Burning More Than Any Time in Recent Millennia." *Proceedings of the National Academy of Sciences* 118: e2103135118. <https://doi.org/10.1073/pnas.2103135118>.
- Hilmers, T., N. Friess, C. Bässler, et al. 2018. "Biodiversity Along Temperate Forest Succession." *Journal of Applied Ecology* 55: 2756–2766. <https://doi.org/10.1111/1365-2664.13238>.
- Hongmao, L., X. Zaifu, X. Youkai, and W. Jinxiu. 2002. "Practice of Conserving Plant Diversity Through Traditional Beliefs: A Case Study in Xishuangbanna, Southwest China." *Biodiversity and Conservation* 11: 705–713. <https://doi.org/10.1023/A:1015532230442>.
- Hubbell, S. P., F. He, R. Condit, L. Borda-de-Água, J. Kellner, and H. ter Steege. 2008. "How Many Tree Species Are There in the Amazon and How Many of Them Will Go Extinct?" *Proceedings of the National Academy of Sciences* 105: 11498–11504. <https://doi.org/10.1073/pnas.0801915105>.
- Huebner, C. D., A. E. Regula, and D. W. McGill. 2018. "Germination, Survival, and Early Growth of Three Invasive Plants in Response to Five Forest Management Regimes Common to US Northeastern Deciduous Forests." *Forest Ecology and Management* 425: 100–118. <https://doi.org/10.1016/j.foreco.2018.05.037>.
- Hulme, P. E. 2009. "Trade, Transport and Trouble: Managing Invasive Species Pathways in an Era of Globalization." *Journal of Applied Ecology* 46: 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>.
- Hutchings, M. J., and E. A. C. Price. 1999. "*Glechoma hederacea* L. (*Nepeta glechoma* Benth., *N. hederacea* (L.) Trev.)." *Journal of Ecology* 87: 347–364.
- Iannone, B., S. Carnevale, M. Main, et al. 2020. "Invasive Species Terminology: Standardizing for Stakeholder Education." *Journal of Extension* 58: 27.
- Iler, A. M., P. J. CaraDonna, J. R. K. Forrest, and E. Post. 2021. "Demographic Consequences of Phenological Shifts in Response to Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 52: 221–245. <https://doi.org/10.1146/annurev-ecolsys-011921-032939>.
- Jefferson, R. G. 2008. "Biological Flora of the British Isles: *Mercurialis perennis* L." *Journal of Ecology* 96, no. 2: 386–412. <https://doi.org/10.1111/j.1365-2745.2007.01348.x>.
- Jia, S., X. Wang, Z. Hao, and R. Bagchi. 2022. "The Effects of Natural Enemies on Herb Diversity in a Temperate Forest Depend on Species Traits and Neighbouring Tree Composition." *Journal of Ecology* 110: 2615–2627. <https://doi.org/10.1111/1365-2745.13973>.
- Johnson, S. E., K. L. Amatangelo, P. A. Townsend, and D. M. Waller. 2016. "Large, Connected Floodplain Forests Prone to Flooding Best Sustain Plant Diversity." *Ecology* 97: 3019–3030. <https://doi.org/10.1002/ecy.1556>.
- Johnson, S. E., and D. M. Waller. 2013. "Influence of Dam Regulation on 55-Year Canopy Shifts in Riparian Forests." *Canadian Journal of Forest Research* 43: 159–170. <https://doi.org/10.1139/cjfr-2012-0390>.
- Jones, K. R., O. Venter, R. A. Fuller, et al. 2018. "One-Third of Global Protected Land Is Under Intense Human Pressure." *Science* 360: 788–791. <https://doi.org/10.1126/science.aap9565>.
- Jones, M. M., H. Tuomisto, D. B. Clark, and P. Olivas. 2006. "Effects of Mesoscale Environmental Heterogeneity and Dispersal Limitation on Floristic Variation in Rain Forest Ferns." *Journal of Ecology* 94, no. 1: 181–195. <https://doi.org/10.1111/j.1365-2745.2005.01071.x>.
- Joppa, L. N., P. Visconti, C. N. Jenkins, and S. L. Pimm. 2013. "Achieving the Convention on Biological Diversity's Goals for Plant Conservation." *Science* 341: 1100–1103. <https://doi.org/10.1126/science.1241706>.
- Kambach, S., F. M. Sabatini, F. Attorre, et al. 2023. "Climate-Trait Relationships Exhibit Strong Habitat Specificity in Plant Communities Across Europe." *Nature Communications* 14: 712. <https://doi.org/10.1038/s41467-023-36240-6>.
- Karban, R., and C. C. Karban. 2024. "Floristic Changes Following the Chestnut Blight May Be Delayed for Decades." *PLoS One* 19: e0306748. <https://doi.org/10.1371/journal.pone.0306748>.
- Keddy, P. A., and B. Shipley. 1989. "Competitive Hierarchies in Herbaceous Plant Communities." *Oikos* 54: 234–241. <https://doi.org/10.2307/3565272>.
- Kemppinen, J., P. Niittynen, P. C. le Roux, et al. 2021. "Consistent Trait–Environment Relationships Within and Across Tundra Plant Communities." *Nature Ecology & Evolution* 5: 458–467. <https://doi.org/10.1038/s41559-021-01396-1>.
- Kermavnar, J., L. Kutnar, and A. Marinšek. 2021. "Disentangling the Ecological Determinants of Species and Functional Trait Diversity in Herb-Layer Plant Communities in European Temperate Forests." *Forests* 12: 552. <https://doi.org/10.3390/f12050552>.
- Kern, C. C., R. A. Montgomery, P. B. Reich, and T. F. Strong. 2014. "Harvest-Created Canopy Gaps Increase Species and Functional Trait Diversity of the Forest Ground-Layer Community." *Forest Science* 60: 335–344. <https://doi.org/10.5849/forsci.13-015>.
- Kleidon, A., and H. A. Mooney. 2000. "A Global Distribution of Biodiversity Inferred From Climatic Constraints: Results From a Process-Based Modelling Study." *Global Change Biology* 6: 507–523. <https://doi.org/10.1046/j.1365-2486.2000.00332.x>.

- Klimeš, A. 2020. *Ecological Differences Between Herbs and Woody Plants, and Evolution of the Herbaceous Habit*. Faculty of Science, Charles University.
- Klooster, W. S., K. J. K. Gandhi, L. C. Long, K. I. Perry, K. B. Rice, and D. A. Herms. 2018. "Ecological Impacts of Emerald Ash Borer in Forests at the Epicenter of the Invasion in North America." *Forests* 9: 250. <https://doi.org/10.3390/f9050250>.
- Koerner, S. E., M. D. Smith, D. E. Burkepile, et al. 2018. "Change in Dominance Determines Herbivore Effects on Plant Biodiversity." *Nature Ecology & Evolution* 2: 1925–1932. <https://doi.org/10.1038/s41559-018-0696-y>.
- Köster, N., K. Friedrich, J. Nieder, and W. Barthlott. 2009. "Conservation of Epiphyte Diversity in an Andean Landscape Transformed by Human Land Use." *Conservation Biology* 23: 911–919. <https://doi.org/10.1111/j.1523-1739.2008.01164.x>.
- Kreft, H., and W. Jetz. 2007. "Global Patterns and Determinants of Vascular Plant Diversity." *Proceedings of the National Academy of Sciences* 104: 5925–5930. <https://doi.org/10.1073/pnas.0608361104>.
- Krömer, T., H. J. R. Einmann, G. Mendieta-Leiva, and G. Zotz. 2025. "Impact of Land-Use Change on Vascular Epiphytes: A Review." *Plants* 14: 1188. <https://doi.org/10.3390/plants14081188>.
- Kusumoto, B., T. Shiono, M. Miyoshi, et al. 2015. "Functional Response of Plant Communities to Clearcutting: Management Impacts Differ Between Forest Vegetation Zones." *Journal of Applied Ecology* 52: 171–180. <https://doi.org/10.1111/1365-2664.12367>.
- LaManna, J. A., S. A. Mangan, A. Alonso, et al. 2017. "Plant Diversity Increases With the Strength of Negative Density Dependence at the Global Scale." *Science* 356: 1389–1392. <https://doi.org/10.1126/science.aam5678>.
- Landuyt, D., E. De Lombaerde, M. P. Perring, et al. 2019. "The Functional Role of Temperate Forest Understorey Vegetation in a Changing World." *Global Change Biology* 25: 3625–3641. <https://doi.org/10.1111/gcb.14756>.
- Laughlin, D. C. 2014. "The Intrinsic Dimensionality of Plant Traits and Its Relevance to Community Assembly." *Journal of Ecology* 102: 186–193. <https://doi.org/10.1111/1365-2745.12187>.
- Lavorel, S., and E. Garnier. 2002. "Predicting Changes in Community Composition and Ecosystem Functioning From Plant Traits: Revisiting the Holy Grail." *Functional Ecology* 16: 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Leake, J. R. 2005. "Plants Parasitic on Fungi: Unearthing the Fungi in Myco-Heterotrophs and Debunking the 'Saprophytic' Plant Myth." *Mycologist* 19: 113–122. <https://doi.org/10.1017/S0269915X05003046>.
- Leão, T. C. C., C. R. Fonseca, C. A. Peres, and M. Tabarelli. 2014. "Predicting Extinction Risk of Brazilian Atlantic Forest Angiosperms." *Conservation Biology* 28: 1349–1359. <https://doi.org/10.1111/cobi.12286>.
- Lee, B. R., T. K. Miller, C. Rosche, et al. 2022. "Wildflower Phenological Escape Differs by Continent and Spring Temperature." *Nature Communications* 13: 7157. <https://doi.org/10.1038/s41467-022-34936-9>.
- Levine, J. M., and J. HilleRisLambers. 2009. "The Importance of Niches for the Maintenance of Species Diversity." *Nature* 461: 254–257. <https://doi.org/10.1038/nature08251>.
- Linares-Gabriel, A., M. A. Hernández-Chontal, and N. Rodríguez-Orozco. 2025. "*Heliconia* spp.: Breeding Impacts of Tropical Floriculture on Flower Industry." In *Breeding of Ornamental Crops: Annuals and Cut Flowers*, edited by J. M. Al-Khayri, S. M. Jain, and M. A. Wani, 573–590. Springer Nature. https://doi.org/10.1007/978-3-031-78653-2_18.
- Linares-Palomino, R., V. Cardona, E. I. Hennig, et al. 2009. "Non-Woody Life-Form Contribution to Vascular Plant Species Richness in a Tropical American Forest." *Plant Ecology* 201: 87–99. <https://doi.org/10.1007/s11258-008-9505-z>.
- Linares-Palomino, R., A. T. Oliveira-Filho, and R. T. Pennington. 2011. "Neotropical Seasonally Dry Forests: Diversity, Endemism, and Biogeography of Woody Plants." In *Seasonally Dry Tropical Forests: Ecology and Conservation*, edited by R. Dirzo, H. S. Young, H. A. Mooney, and G. Ceballos, 3–21. Island Press/Center for Resource Economics. https://doi.org/10.5822/978-1-61091-021-7_1.
- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. *Invasion Ecology*. 2nd ed. Wiley.
- Loehle, C., K. A. Solarik, D. U. Greene, L. Six, and D. J. H. Sleep. 2021. "Potential Recolonization Benefits of Retention Forestry Practices." *Forest Science* 67: 356–366. <https://doi.org/10.1093/forsci/fxaa054>.
- Lovett, G. M., M. Weiss, A. M. Liebhold, et al. 2016. "Nonnative Forest Insects and Pathogens in the United States: Impacts and Policy Options." *Ecological Applications* 26: 1437–1455. <https://doi.org/10.1890/15-1176>.
- Luján, M., R. M. Lemos, E. Lucas, et al. 2024. "Trials and Tribulations of Neotropical Plant Taxonomy: Pace of Tree Species Description." *Plants, People, Planet* 6: 515–527. <https://doi.org/10.1002/ppp3.10469>.
- Malhi, Y., O. L. Phillips, J. Lloyd, et al. 2002. "An International Network to Monitor the Structure, Composition and Dynamics of Amazonian Forests (RAINFOR)." *Journal of Vegetation Science* 13: 439–450. <https://doi.org/10.1111/j.1654-1103.2002.tb02068.x>.
- Mamadalieva, N. Z. Z., D. K. K. Akramov, L. A. A. Wessjohann, et al. 2021. "The Genus *Lagochilus* (Lamiaceae): A Review of Its Diversity, Ethnobotany, Phytochemistry, and Pharmacology." *Plants* 10: 132. <https://doi.org/10.3390/plants10010132>.
- Mammola, S., I. R. Amorim, M. E. Bichuette, et al. 2020. "Fundamental Research Questions in Subterranean Biology." *Biological Reviews* 95: 1855–1872. <https://doi.org/10.1111/brv.12642>.
- Måren, I. E., J. Kapfer, P. A. Aarrestad, J.-A. Grytnes, and V. Vandvik. 2018. "Changing Contributions of Stochastic and Deterministic Processes in Community Assembly Over a Successional Gradient." *Ecology* 99: 148–157. <https://doi.org/10.1002/ecy.2052>.
- Marschner, P. 2007. "Plant-Microbe Interactions in the Rhizosphere and Nutrient Cycling." In *Nutrient Cycling in Terrestrial Ecosystems*, edited by P. Marschner and Z. Rengel, 159–173. Springer.
- Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. "Functional Richness, Functional and Functional Evenness Divergence: The Primary of Functional Components Diversity." *Oikos* 111: 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- Massante, J. C., L. Götzenberger, K. Takkis, et al. 2019. "Contrasting Latitudinal Patterns in Phylogenetic Diversity Between Woody and Herbaceous Communities." *Scientific Reports* 9, no. 1: 6443. <https://doi.org/10.1038/s41598-019-42827-1>.
- Matsuo, T., M. T. van der Sande, L. Amissah, J. Dabo, S. Mohammed Abdul, and L. Poorter. 2024. "Herbaceous Species and Dry Forest Species Have More Acquisitive Leaf Traits Than Woody Species and Wet Forest Species." *Functional Ecology* 38: 194–205. <https://doi.org/10.1111/1365-2435.14477>.
- McCarthy, B. C. 2014. "The Herbaceous Layer of Eastern Old-Growth Deciduous Forests." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 202–214. Oxford University Press.
- McColl-Gausden, S. C., L. T. Bennett, H. G. Clarke, D. A. Ababei, and T. D. Penman. 2022. "The Fuel–Climate–Fire Conundrum: How Will Fire Regimes Change in Temperate Eucalypt Forests Under Climate Change?" *Global Change Biology* 28: 5211–5226. <https://doi.org/10.1111/gcb.16283>.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. "Rebuilding Community Ecology From Functional Traits." *Trends in Ecology & Evolution* 21: 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>.
- McLauchlan, K. K., P. E. Higuera, J. Miesel, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers."

- Journal of Ecology* 108: 2047–2069. <https://doi.org/10.1111/1365-2745.13403>.
- McMichael, C. N. H., M. B. Bush, J. C. Jiménez, and W. D. Gosling. 2023. “Past Human-Induced Ecological Legacies as a Driver of Modern Amazonian Resilience.” *People and Nature* 5: 1415–1429. <https://doi.org/10.1002/pan3.10510>.
- Meddens, A. J. H., C. A. Kolden, J. A. Lutz, et al. 2018. “Fire Refugia: What Are They, and Why Do They Matter for Global Change?” *Bioscience* 68: 944–954. <https://doi.org/10.1093/biosci/biy103>.
- Meyer, C., P. Weigelt, and H. Kreft. 2016. “Multidimensional Biases, Gaps and Uncertainties in Global Plant Occurrence Information.” *Ecology Letters* 19: 992–1006. <https://doi.org/10.1111/ele.12624>.
- Mölder, A., M. Bernhardt-Römermann, and W. Schmidt. 2008. “Herb-Layer Diversity in Deciduous Forests: Raised by Tree Richness or Beaten by Beech?” *Forest Ecology and Management* 256: 272–281. <https://doi.org/10.1016/j.foreco.2008.04.012>.
- Mollot, G., J. H. Pantel, and T. N. Romanuk. 2017. “The Effects of Invasive Species on the Decline in Species Richness: A Global Meta-Analysis.” In *Advances in Ecological Research*, edited by D. A. Bohan, A. J. Dumbrell, and F. Massol, 61–83. Academic Press. <https://doi.org/10.1016/bs.aecr.2016.10.002>.
- Moss, C. E., W. M. Rankin, and A. G. Tansley. 1910. “The Woodlands of England.” *New Phytologist* 9: 113–149. <https://www.jstor.org/stable/2427132>.
- Mudrak, E. L., S. E. Johnson, and D. M. Waller. 2009. “Forty-Seven Year Changes in Vegetation at the Apostle Islands: Effects of Deer on the Forest Understory.” *Natural Areas Journal* 29: 167–176. <https://doi.org/10.3375/043.029.0209>.
- Muller, R. N. 2014. “Nutrient Relations of the Herbaceous Layer in Deciduous Forest Ecosystems.” In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. S. Gilliam, First ed., 13–34. Oxford University Press.
- Mureithi, S. M., A. Verdoodt, J. T. Njoka, C. K. Gachene, F. Warinwa, and E. Van Ranst. 2016. “Impact of Community Conservation Management on Herbaceous Layer and Soil Nutrients in a Kenyan Semi-Arid Savannah.” *Land Degradation & Development* 27: 1820–1830. <https://doi.org/10.1002/ldr.2315>.
- Murphy, S. J., K. Salpeter, and L. S. Comita. 2016. “Higher β -Diversity Observed for Herbs Over Woody Plants Is Driven by Stronger Habitat Filtering in a Tropical Understory.” *Ecology* 97: 2074–2084. <https://doi.org/10.1890/15-1801.1>.
- Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. “Seed Dispersal by White-Tailed Deer: Implications for Long-Distance Dispersal, Invasion, and Migration of Plants in Eastern North America.” *Oecologia* 139: 35–44. <https://doi.org/10.1007/s00442-003-1474-2>.
- Nair, K. P. 2019. “Production, Marketing, and Economics of Ginger.” In *Turmeric (Curcuma longa L.) and Ginger (Zingiber officinale Rosc.) - World's Invaluable Medicinal Spices: The Agronomy and Economy of Turmeric and Ginger*, edited by K. P. Nair, 493–518. Springer International Publishing. https://doi.org/10.1007/978-3-030-29189-1_24.
- Nakazono, E. M., E. M. Bruna, and R. C. G. Mesquita. 2004. “Experimental Harvesting of the Non-Timber Forest Product *Ischnosiphon polyphyllus* in Central Amazonia.” *Forest Ecology and Management* 190: 219–225. <https://doi.org/10.1016/j.foreco.2003.10.013>.
- Neufield, H. S., and D. R. Young. 2014. “Ecophysiology of the Herbaceous Layer in Temperate Deciduous Forests.” In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. S. Gilliam, First ed., 35–91. Oxford University Press.
- Nieder, J., S. Engwald, and W. Barthlott. 1999. “Patterns of Neotropical Epiphyte Diversity.” *Selbyana* 20: 66–75. <https://www.jstor.org/stable/41760009>.
- Nogueira-Filho, S. L. G., S. S. C. Nogueira, and J. M. V. Fragoso. 2009. “Ecological Impacts of Feral Pigs in the Hawaiian Islands.” *Biodiversity and Conservation* 18: 3677–3683. <https://doi.org/10.1007/s10551-009-9680-9>.
- Noualhuquet, M., T. T. Work, C. A. Nock, S. E. Macdonald, I. Aubin, and N. J. Fenton. 2024. “Functional Responses of Understory Plants to Natural Disturbance-Based Management in Eastern and Western Canada.” *Ecological Applications* 34: e3011. <https://doi.org/10.1002/eap.3011>.
- Oswalt, C. M., S. Fei, Q. Guo, et al. 2015. “A Subcontinental View of Forest Plant Invasions.” *NeoBiota* 24: 49–54. <https://doi.org/10.3897/neobiota.24.4526>.
- Parmesan, C., and M. E. Hanley. 2015. “Plants and Climate Change: Complexities and Surprises.” *Annals of Botany* 116: 849–864. <https://doi.org/10.1093/aob/mcv169>.
- Pastur, G. M., M. V. Lencinas, J. Escobar, P. Quiroga, L. Malmierca, and M. Lizarralde. 2006. “Understorey Succession in Nothofagus Forests in Tierra del Fuego (Argentina) Affected by *Castor canadensis*.” *Applied Vegetation Science* 9: 143–154. [https://doi.org/10.1658/1402-2001\(2006\)9\[143:USINFI\]2.0.CO;2](https://doi.org/10.1658/1402-2001(2006)9[143:USINFI]2.0.CO;2).
- Peacock, J., T. B. Baker, S. L. Lewis, G. Lopez-Gonzalez, and O. L. Phillips. 2007. “The RAINFOR Database: Monitoring Forest Biomass and Dynamics.” *Journal of Vegetation Science* 18: 535–542. <https://doi.org/10.1111/j.1654-1103.2007.tb02568.x>.
- Peet, R., M. Lee, F. Boyle, T. Wentworth, M. Schafale, and A. Weakley. 2012. “Vegetation-Plot Database of the Carolina Vegetation Survey.” *Biodiversity & Ecology* 4: 243–253. <https://doi.org/10.7809/b-e.00081>.
- Peet, R. K., K. A. Palmquist, T. R. Wentworth, M. P. Schafale, A. S. Weakley, and M. T. Lee. 2018. “Carolina Vegetation Survey: An Initiative to Improve Regional Implementation of the U.S.” *National Vegetation Classification*. *Phytocoenologia* 48: 171–179. <https://doi.org/10.1127/phyto/2017/0168>.
- Peet, R. K., T. R. Wentworth, and P. S. White. 1998. “A Flexible, Multipurpose Method for Recording Vegetation Composition and Structure.” *Castanea* 63: 262–274. <https://www.jstor.org/stable/4033979>.
- Perea, R., J. W. Schroeder, and R. Dirzo. 2022. “The Herbaceous Understory Plant Community in the Context of the Overstory: An Overlooked Component of Tropical Diversity.” *Diversity* 14: 800. <https://doi.org/10.3390/d14100800>.
- Pereyra, P. J. 2016. “Revisiting the Use of the Invasive Species Concept: An Empirical Approach.” *Austral Ecology* 41: 519–528. <https://doi.org/10.1111/aec.12340>.
- Perring, M. P., M. Bernhardt-Römermann, L. Baeten, et al. 2018. “Global Environmental Change Effects on Plant Community Composition Trajectories Depend Upon Management Legacies.” *Global Change Biology* 24: 1722–1740. <https://doi.org/10.1111/gcb.14030>.
- Peter, D. H., and T. B. Harrington. 2018. “Effects of Forest Harvesting, Logging Debris, and Herbicides on the Composition, Diversity and Assembly of a Western Washington, USA Plant Community.” *Forest Ecology and Management* 417: 18–30. <https://doi.org/10.1016/j.foreco.2018.01.045>.
- Peterken, G. 1993. *Woodland Conservation and Management*. 2nd ed. Chapman & Hall.
- Petruski, L. M., S. F. Owen, G. D. Constantz, and J. T. Anderson. 2019. “Changes in Flowering Phenology of *Cardamine concatenata* and *Erythronium americanum* Over 111 Years in the Central Appalachians.” *Plant Ecology* 220: 817–828. <https://doi.org/10.1007/s11258-019-00956-7>.
- Pfeiffer, T., L. Schmidt, A. M. Roschanski, and M. Schnittler. 2019. “A Battle of the Sexes? Sex Ratio and Performance at Small Scales in

- Dioecious *Mercurialis perennis*." *Acta Oecologica* 100: 103462. <https://doi.org/10.1016/j.actao.2019.103462>.
- Piao, S., Q. Liu, A. Chen, et al. 2019. "Plant Phenology and Global Climate Change: Current Progresses and Challenges." *Global Change Biology* 25: 1922–1940. <https://doi.org/10.1111/gcb.14619>.
- Pizano, M. 2023. "Innovation and Sustainability in South American Floriculture." *Acta Horticulturae* 1368: 77–84. <https://doi.org/10.17660/ActaHortic.2023.1368.11>.
- Poulsen, A. D. 1996. "Species Richness and Density of Ground Herbs Within a Plot of Lowland Rainforest in North-West Borneo." *Journal of Tropical Ecology* 12: 177–190. <https://doi.org/10.1017/S0266467400009408>.
- Pouteau, R., J. Picard, C. Doumenge, et al. 2024. "The Puzzling Ecology of African Marantaceae Forests." *American Journal of Botany* 111: e16320. <https://doi.org/10.1002/ajb2.16320>.
- Qin, S., J. Li, H.-H. Chen, et al. 2009. "Isolation, Diversity, and Antimicrobial Activity of Rare Actinobacteria From Medicinal Plants of Tropical Rain Forests in Xishuangbanna, China." *Applied and Environmental Microbiology* 75: 6176–6186. <https://doi.org/10.1128/AEM.01034-09>.
- Queenborough, S. A., K. M. Burnet, W. J. Sutherland, A. R. Watkinson, and R. P. Freckleton. 2011. "From Meso- To Macroscale Population Dynamics: A New Density-Structured Approach." *Methods in Ecology and Evolution* 2: 289–302. <https://doi.org/10.1111/j.2041-210X.2010.00075.x>.
- Radhamoni, H. V. N., S. A. Queenborough, A. Z. A. Arietta, et al. 2023. "Local- and Landscape-Scale Drivers of Terrestrial Herbaceous Plant Diversity Along a Tropical Rainfall Gradient in Western Ghats, India." *Journal of Ecology* 111: 1021–1036. <https://doi.org/10.1111/1365-2745.14075>.
- Radhamoni, H. V. N., J. Vleminckx, M. N. Umaña, et al. 2025. "Beta-Diversity of Herbaceous Versus Woody Plant Communities Across a Tropical Rainfall Gradient." *Journal of Vegetation Science* 36: e70034. <https://doi.org/10.1111/jvs.70034>.
- Ralte, L., H. Sailo, and Y. T. Singh. 2024. "Ethnobotanical Study of Medicinal Plants Used by the Indigenous Community of the Western Region of Mizoram." *India. Journal of Ethnobiology and Ethnomedicine* 20: 2. <https://doi.org/10.1186/s13002-023-00642-z>.
- Ram, B., and A. Chawla. 2024. "Shrubs Exhibit Competitive Interactions With Herbaceous Plants and Shape Community Assemblage and Functional Composition in the Alpine Western Himalaya." *Journal of Vegetation Science* 35: e13269. <https://doi.org/10.1111/jvs.13269>.
- Rao, R. R. 2012. "Plant Taxonomy in Tropical Countries: A Plea for Urgent Resurrection." *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences* 82: 259–264. <https://doi.org/10.1007/s40011-012-0043-z>.
- Raunkiaer, C. C. 1934. "The Life Forms of Plants and Statistical Plant Geography." *American Midland Naturalist* 15: 786.
- Rivers, M., A. C. Newton, S. Oldfield, and G. T. A. Contributors. 2023. "Scientists' Warning to Humanity on Tree Extinctions." *Plants, People, Planet* 5: 466–482. <https://doi.org/10.1002/ppp3.10314>.
- Roberts, M. R. 2002. "Effects of Forest Plantation Management on Herbaceous-Layer Composition and Diversity." *Canadian Journal of Botany* 80: 378–389. <https://doi.org/10.1139/b02-023>.
- Roberts, M. R. 2004. "Response of the Herbaceous Layer to Natural Disturbance in North American Forests." *Canadian Journal of Botany* 82: 1273–1283. <https://doi.org/10.1139/b04-091>.
- Roberts, M. R., and F. S. Gilliam. 2014. "Response of the Herbaceous Layer to Disturbance in Eastern Forests." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 320–339. Oxford University Press.
- Rolhauser, A. G., D. M. Waller, and C. M. Tucker. 2021. "Complex Trait–Environment Relationships Underlie the Structure of Forest Plant Communities." *Journal of Ecology* 109: 3794–3806. <https://doi.org/10.1111/1365-2745.13757>.
- Römer, G., J. P. Dahlgren, R. Salguero-Gómez, I. M. Stott, and O. R. Jones. 2024. "Plant Demographic Knowledge Is Biased Towards Short-Term Studies of Temperate-Region Herbaceous Perennials." *Oikos* 2024: e10250. <https://doi.org/10.1111/oik.10250>.
- Rooney, T. P., and D. M. Waller. 2003. "Direct and Indirect Effects of White-Tailed Deer in Forest Ecosystems." *Forest Ecology and Management* 181: 165–176. [https://doi.org/10.1016/S0378-1127\(03\)00130-0](https://doi.org/10.1016/S0378-1127(03)00130-0).
- Rosenblad, K. C., K. C. Baer, and D. D. Ackerly. 2023. "Climate Change, Tree Demography, and Thermophilization in Western US Forests." *Proceedings of the National Academy of Sciences* 120: e2301754120. <https://doi.org/10.1073/pnas.2301754120>.
- Roumet, C., M. Birouste, C. Picon-Cochard, et al. 2016. "Root Structure–Function Relationships in 74 Species: Evidence of a Root Economics Spectrum Related to Carbon Economy." *New Phytologist* 210: 815–826.
- Royo, A. A., and W. P. Carson. 2008. "Direct and Indirect Effects of a Dense Understory on Tree Seedling Recruitment in Temperate Forests: Habitat-Mediated Predation Versus Competition." *Canadian Journal of Forest Research* 38: 1634–1645. <https://doi.org/10.1111/nph.13828>.
- Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. "Pervasive Interactions Between Ungulate Browsers and Disturbance Regimes Promote Temperate Forest Herbaceous Diversity." *Ecology* 91: 93–105. <https://doi.org/10.1890/08-1680.1>.
- Rożek, K., K. Rola, J. Błazkowski, and S. Zubek. 2019. "Associations of Root-Inhabiting Fungi With Herbaceous Plant Species of Temperate Forests in Relation to Soil Chemical Properties." *Science of the Total Environment* 649: 1573–1579. <https://doi.org/10.1016/j.scitotenv.2018.08.350>.
- Rundel, P. W., M. R. Sharifi, A. C. Gibson, and K. J. Esler. 1998. "Structural and Physiological Adaptation to Light Environments in Neotropical *Heliconia* (Heliconiaceae)." *Journal of Tropical Ecology* 14: 789–801. <https://doi.org/10.1017/S0266467498000571>.
- Sabatini, F. M., J. I. Burton, R. M. Scheller, K. L. Amatangelo, and D. J. Mladenoff. 2014. "Functional Diversity of Ground-Layer Plant Communities in Old-Growth and Managed Northern Hardwood Forests." *Applied Vegetation Science* 17: 398–407. <https://doi.org/10.1111/avsc.12083>.
- Schellenberger Costa, D., G. Zotz, A. Hemp, and M. Kleyer. 2018. "Trait Patterns of Epiphytes Compared to Other Plant Life-Forms Along a Tropical Elevation Gradient." *Functional Ecology* 32: 2073–2084. <https://doi.org/10.1111/1365-2435.13121>.
- Schmidt, J. P., J. Cruse-Sanders, J. L. Chamberlain, S. Ferreira, and J. A. Young. 2019. "Explaining Harvests of Wild-Harvested Herbaceous Plants: American Ginseng as a Case Study." *Biological Conservation* 231: 139–149. <https://doi.org/10.1016/j.biocon.2019.01.006>.
- Schnitzer, S. A., F. E. Putz, F. Bongers, and K. Kroening. 2015. "The Past, Present, and Potential Future of Liana Ecology." In *Ecology of Lianas*, edited by S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, 1–10. John Wiley & Sons. <https://doi.org/10.1002/9781118392409.ch1>.
- Schoennagel, T., E. A. H. Smithwick, and M. G. Turner. 2008. "Landscape Heterogeneity Following Large Fires: Insights From Yellowstone National Park, USA." *International Journal of Wildland Fire* 17: 742. <https://doi.org/10.1071/WF07146>.
- Schulze, E. D., G. Aas, G. W. Grimm, et al. 2016. "A Review on Plant Diversity and Forest Management of European Beech Forests." *European Journal of Forest Research* 135: 51–67. <https://doi.org/10.1007/s10342-015-0922-y>.

- Scott, E. R., M. Uriarte, and E. M. Bruna. 2022. "Delayed Effects of Climate on Vital Rates Lead to Demographic Divergence in Amazonian Forest Fragments." *Global Change Biology* 28: 463–479. <https://doi.org/10.1111/gcb.15900>.
- Seghier, J. 1995. "The Rooting Patterns of Woody and Herbaceous Plants in a Savanna; Are They Complementary or in Competition?" *African Journal of Ecology* 33: 358–365. <https://doi.org/10.1111/j.1365-2028.1995.tb01045.x>.
- Shannon, S., S. L. Flory, and H. Reynolds. 2012. "Competitive Context Alters Plant–Soil Feedback in an Experimental Woodland Community." *Oecologia* 169: 235–243. <https://doi.org/10.1007/s00442-011-2195-6>.
- Shennan-Farpon, Y., P. Visconti, and K. Norris. 2021. "Detecting Ecological Thresholds for Biodiversity in Tropical Forests: Knowledge Gaps and Future Directions." *Biotropica* 53: 1276–1289. <https://doi.org/10.1111/btp.12999>.
- Shipley, B., F. De Bello, J. H. C. Cornelissen, E. Laliberté, D. C. Laughlin, and P. B. Reich. 2016. "Reinforcing Loose Foundation Stones in Trait-Based Plant Ecology." *Oecologia* 180: 923–931. <https://doi.org/10.1007/s00442-016-3549-x>.
- Šimová, I., C. Violle, J.-C. Svenning, et al. 2018. "Spatial Patterns and Climate Relationships of Major Plant Traits in the New World Differ Between Woody and Herbaceous Species." *Journal of Biogeography* 45: 895–916. <https://doi.org/10.1111/jbi.13171>.
- Small, C. J., and B. C. McCarthy. 2002. "Spatial and Temporal Variability of Herbaceous Vegetation in an Eastern Deciduous Forest." *Plant Ecology* 164: 37–48. <https://doi.org/10.1023/A:1021209528643>.
- Smith, L. M., and H. L. Reynolds. 2015. "Extended Leaf Phenology, Allelopathy, and Inter-Population Variation Influence Invasion Success of an Understory Forest Herb." *Biological Invasions* 17: 2299–2313. <https://doi.org/10.1007/s10530-015-0876-5>.
- Smith, S. A., and J. M. Beaulieu. 2009. "Life History Influences Rates of Climatic Niche Evolution in Flowering Plants." *Proceedings of the Royal Society B: Biological Sciences* 276: 4345–4352. <https://doi.org/10.1098/rspb.2009.1176>.
- Smith, S. A., and M. J. Donoghue. 2008. "Rates of Molecular Evolution Are Linked to Life History in Flowering Plants." *Science (New York, N.Y.)* 322: 86–89. <https://doi.org/10.1126/science.1163197>.
- Spicer, M. E., H. Mellor, and W. P. Carson. 2020. "Seeing Beyond the Trees: A Comparison of Tropical and Temperate Plant Growth Forms and Their Vertical Distribution." *Ecology* 101: e02974. <https://doi.org/10.1002/ecy.2974>.
- Spicer, M. E., H. V. N. Radhamoni, M. C. Duguid, S. A. Queenborough, and L. S. Comita. 2022. "Herbaceous Plant Diversity in Forest Ecosystems: Patterns, Mechanisms, and Threats." *Plant Ecology* 223: 117–129. <https://doi.org/10.1007/s11258-021-01202-9>.
- Standish, R. J., A. W. Robertson, and P. A. Williams. 2001. "The Impact of an Invasive Weed *Tradescantia fluminensis* on Native Forest Regeneration." *Journal of Applied Ecology* 38, no. 6: 1253–1263. <https://doi.org/10.1046/j.0021-8901.2001.00673.x>.
- Stefanowicz, A. M., P. Kapusta, M. Stanek, K. Rola, and S. Zubek. 2022. "Herbaceous Plant Species Support Soil Microbial Performance in Deciduous Temperate Forests." *Science of the Total Environment* 810: 151313. <https://doi.org/10.1016/j.scitotenv.2021.151313>.
- Stepp, J. R. 2018. "Ethnoecology and Medicinal Plants of the Highland Maya: An Introduction." In *Ethnoecology and Medicinal Plants of the Highland Maya*, edited by J. R. Stepp, 1–10. Springer International Publishing.
- Stewart, S. M., and K. M. Byrne. 2025. "Is Reinforcement a Viable Conservation Strategy for the Endangered Perennial Herb, *Astragalus applegatei*?" *Restoration Ecology* 33: e14314. <https://doi.org/10.1111/rec.14314>.
- Stokely, T. D., U. G. Kormann, J. Verschuyt, et al. 2022. "Experimental Evaluation of Herbicide Use on Biodiversity, Ecosystem Services and Timber Production Trade-Offs in Forest Plantations." *Journal of Applied Ecology* 59: 52–66. <https://doi.org/10.1111/1365-2664.13936>.
- Stroud, S., M. Fennell, J. Mitchley, S. Lydon, J. Peacock, and K. L. Bacon. 2022. "The Botanical Education Extinction and the Fall of Plant Awareness." *Ecology and Evolution* 12: e9019. <https://doi.org/10.1002/ece3.9019>.
- Stump, S. M., and L. S. Comita. 2018. "Interspecific Variation in Conspecific Negative Density Dependence Can Make Species Less Likely to Coexist." *Ecology Letters* 21: 1541–1551. <https://doi.org/10.1111/ele.13135>.
- Stump, S. M., and L. S. Comita. 2020. "Differences Among Species in Seed Dispersal and Conspecific Neighbor Effects Can Interact to Influence Coexistence." *Theoretical Ecology* 13: 551–581. <https://doi.org/10.1007/s12080-020-00468-5>.
- Sutherland, W. J., W. M. Adams, R. B. Aronson, et al. 2009. "One Hundred Questions of Importance to the Conservation of Global Biological Diversity." *Conservation Biology* 23: 557–567. <https://doi.org/10.1111/j.1523-1739.2009.01212.x>.
- Sutherland, W. J., E. Fleishman, M. B. Mascia, J. Pretty, and M. A. Rudd. 2011. "Methods for Collaboratively Identifying Research Priorities and Emerging Issues in Science and Policy." *Methods in Ecology and Evolution* 2: 238–247. <https://doi.org/10.1111/j.2041-210X.2010.00083.x>.
- Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, et al. 2013. "Identification of 100 Fundamental Ecological Questions." *Journal of Ecology* 101: 58–67. <https://doi.org/10.1111/1365-2745.12025>.
- Sutherland, W. J., D. Goulson, S. G. Potts, and L. V. Dicks. 2011. "Quantifying the Impact and Relevance of Scientific Research." *PLoS One* 6: e27537. <https://doi.org/10.1371/journal.pone.0027537>.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, et al. 2010. "The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites." *Frontiers in Ecology and the Environment* 9: 117–125. <https://doi.org/10.1890/090157>.
- Takahashi, K. 2004. "Crown Architecture of the Ginger *Alpinia Scabra* (Zingiberaceae) in a Tropical Submontane Forest, Indonesia *Alpinia Scabra*." *Tropics* 14: 65–73. <https://doi.org/10.3759/tropics.14.65>.
- Taylor, A., G. Zotz, P. Weigelt, et al. 2022. "Vascular Epiphytes Contribute Disproportionately to Global Centres of Plant Diversity." *Global Ecology and Biogeography* 31: 62–74. <https://doi.org/10.1111/geb.13411>.
- Taylor, K., and P. Rowland. 2010. "Biological Flora of the British Isles: *Stachys sylvatica* L." *Journal of Ecology* 98, no. 6: 1476–1489. <https://doi.org/10.1111/j.1365-2745.2010.01725.x>.
- Thrippleton, T., H. Bugmann, K. Kramer-Priewasser, and R. S. Snell. 2016. "Herbaceous Understorey: An Overlooked Player in Forest Landscape Dynamics?" *Ecosystems* 19: 1240–1254. <https://doi.org/10.1007/s10021-016-9999-5>.
- Tian, K., P. Chai, Y. Wang, et al. 2023. "Species Diversity Pattern and Its Drivers of the Understory Herbaceous Plants in a Chinese Subtropical Forest." *Frontiers in Ecology and Evolution* 10: 1113742. <https://doi.org/10.3389/fevo.2022.1113742>.
- Ticktin, T. 2004. "The Ecological Implications of Harvesting Non-Timber Forest Products." *Journal of Applied Ecology* 41: 11–21. <https://doi.org/10.1111/j.1365-2664.2004.00859.x>.
- Ticktin, T., K. Kindscher, S. Souther, et al. 2018. "Ecological Dimensions of Nontimber Forest Product Harvest. In: Chamberlain, James L.; Emery, Marla R.; Patel-Weynand, Toral, Eds. 2018. Assessment of Nontimber Forest Products in the United States Under Changing Conditions. Gen. Tech. Rep. SRS-232. Asheville, NC: U.S." *Department of Agriculture, Forest Service, Southern Research Station* 2018: 60–81.
- Toju, H., S. Yamamoto, H. Sato, and A. S. Tanabe. 2013. "Sharing of Diverse Mycorrhizal and Root-Endophytic Fungi Among Plant Species

- in an Oak-Dominated Cool-Temperate Forest." *PLoS One* 8: e78248. <https://doi.org/10.1371/journal.pone.0078248>.
- Tölgyesi, C., O. Valkó, B. Deák, et al. 2018. "Tree-Herb Co-Existence and Community Assembly in Natural Forest-Steppe Transitions." *Plant Ecology and Diversity* 11: 465–477. <https://doi.org/10.1080/17550874.2018.1544674>.
- Trindade, W. C. F., and M. C. M. Marques. 2024. "The Invisible Species: Big Data Unveil Coverage Gaps in the Atlantic Forest Hotspot." *Diversity and Distributions* 30: e13931. <https://doi.org/10.1111/ddi.13931>.
- van Andel, T., and R. Havinga. 2008. "Sustainability Aspects of Commercial Medicinal Plant Harvesting in Suriname." *Forest Ecology and Management* 256: 1540–1545. <https://doi.org/10.1016/j.foreco.2008.06.031>.
- Vandenbergh, C., F. Freléchoux, and A. Buttler. 2008. "The Influence of Competition From Herbaceous Vegetation and Shade on Simulated Browsing Tolerance of Coniferous and Deciduous Saplings." *Oikos* 117: 415–423. <https://doi.org/10.1111/j.2007.0030-1299.16264.x>.
- Vandenbergh, C., F. Freléchoux, F. Gadallah, and A. Buttler. 2006. "Competitive Effects of Herbaceous Vegetation on Tree Seedling Emergence, Growth and Survival: Does Gap Size Matter?" *Journal of Vegetation Science* 17: 481–488.
- Vandepitte, K., I. Roldán-Ruiz, L. Leus, H. Jacquemyn, and O. Honnay. 2009. "Canopy Closure Shapes Clonal Diversity and Fine-Scale Genetic Structure in the Dioecious Understorey Perennial *Mercurialis perennis*." *Journal of Ecology* 97: 404–414. <https://doi.org/10.1111/j.1654-1103.2006.tb02469.x>.
- Vanneste, T., A. Valdés, K. Verheyen, et al. 2019. "Functional Trait Variation of Forest Understorey Plant Communities Across Europe." *Basic and Applied Ecology* 34: 1–14. <https://doi.org/10.1016/j.baae.2018.09.004>.
- Vellend, M. 2005. "Land-Use History and Plant Performance in Populations of *Trillium grandiflorum*." *Biological Conservation* 124, no. 2: 217–224. <https://doi.org/10.1016/j.biocon.2005.01.027>.
- Vellend, M. 2016. *The Theory of Ecological Communities*. Princeton University Press. <https://doi.org/10.1515/9781400883790>.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. "Dispersal of Trillium Seeds by Deer: Implications for Long-Distance Migration of Forest Herbs." *Ecology* 84: 1067–1072. [https://doi.org/10.1890/0012-9658\(2003\)084\[1067:DOTSBD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1067:DOTSBD]2.0.CO;2).
- Verbeeck, H., H. P. T. De Deurwaerder, E. Kearsley, et al. 2024. "Towards a Liana Plant Functional Type for Vegetation Models." *Ecological Modelling* 498: 110901. <https://doi.org/10.1016/j.ecolmodel.2024.110901>.
- Veresoglou, S. D., M. Wulf, and M. C. Rillig. 2017. "Facilitation Between Woody and Herbaceous Plants That Associate With Arbuscular Mycorrhizal Fungi in Temperate European Forests." *Ecology and Evolution* 7: 1181–1189. <https://doi.org/10.1002/ece3.2757>.
- Verheyen, K., B. Bossuyt, O. Honnay, and M. Hermy. 2003. "Herbaceous Plant Community Structure of Ancient and Recent Forests in Two Contrasting Forest Types." *Basic and Applied Ecology* 4: 537–546. <https://doi.org/10.1078/1439-1791-00210>.
- Waller, D., K. Amatangelo, S. Johnson, and D. Rogers. 2012. "Wisconsin Vegetation Database – Plant Community Survey and Resurvey Data From the Wisconsin Plant Ecology Laboratory." *Biodiversity & Ecology* 4: 255–264. <https://doi.org/10.7809/b-e.00082>.
- Waller, D. M. 2014. "Effects of Deer on Forest Herb Layers." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 369–399. Oxford University Press.
- Wang, R., Y. Chen, H. Zhang, et al. 2025. "Plant-Microbe Interactions Drive the Rhizosphere Microbial Assembly and Nitrogen Cycling in a Subtropical Forest." *Functional Ecology* 39: 1274–1287. <https://doi.org/10.1111/1365-2435.70025>.
- Warren, R. J., and M. A. Bradford. 2011. "The Shape of Things to Come: Woodland Herb Niche Contraction Begins During Recruitment in Mesic Forest Microhabitat." *Proceedings of the Royal Society B: Biological Sciences* 278: 1390–1398. <https://doi.org/10.1098/rspb.2010.1886>.
- Wassel, A. C., and J. A. Myers. 2025. "Pawpaws Prevent Predictability: A Locally Dominant Tree Alters Understory Beta-Diversity and Community Assembly." *Ecosphere* 16: e70115. <https://doi.org/10.1002/ecs2.70115>.
- Wavrek, M., J. M. Heberling, S. Fei, and S. Kalisz. 2017. "Herbaceous Invaders in Temperate Forests: A Systematic Review of Their Ecology and Proposed Mechanisms of Invasion." *Biological Invasions* 19: 3079–3097. <https://doi.org/10.1007/s10530-017-1456-7>.
- Webster, C. R., Y. L. Dickinson, J. I. Burton, et al. 2018. "Promoting and Maintaining Diversity in Contemporary Hardwood Forests: Confronting Contemporary Drivers of Change and the Loss of Ecological Memory." *Forest Ecology and Management* 421: 98–108. <https://doi.org/10.1016/j.foreco.2018.01.010>.
- Weemstra, M., L. Mommer, E. J. W. Visser, et al. 2016. "Towards a Multidimensional Root Trait Framework: A Tree Root Review." *New Phytologist* 211: 1159–1169. <https://doi.org/10.1111/nph.14003>.
- Welch, N. T., J. M. Belmont, and J. C. Randolph. 2007. "Summer Ground Layer Biomass and Nutrient Contribution to Above-Ground Litter in an Indiana Temperate Deciduous Forest." *American Midland Naturalist* 157: 11–26. [https://doi.org/10.1674/0003-0031\(2007\)157\[11:SGLBAN\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2007)157[11:SGLBAN]2.0.CO;2).
- Whigham, D. F. 2004. "Ecology of Woodland Herbs in Temperate Deciduous Forests." *Annual Review of Ecology, Evolution, and Systematics* 35: 583–621. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105708>.
- Wiegmann, S. M., and D. M. Waller. 2006. "Fifty Years of Change in Northern Upland Forest Understories: Identity and Traits of "Winner" and "Loser" Plant Species." *Biological Conservation* 129: 109–123. <https://doi.org/10.1016/j.biocon.2005.10.027>.
- Winkler, E., and B. Schmid. 1995. "Clonal Strategies of Herbaceous Plant Species: A Simulation Study on Population Growth and Competition." *Abstracta Botanica* 19: 17–28. <https://www.jstor.org/stable/43519476>.
- Winsome, T., L. C. R. Silva, K. M. Scow, T. A. Doane, R. F. Powers, and W. R. Horwath. 2017. "Plant-Microbe Interactions Regulate Carbon and Nitrogen Accumulation in Forest Soils." *Forest Ecology and Management* 384: 415–423. <https://doi.org/10.1016/j.foreco.2016.10.036>.
- Wolf, S., M. D. Mahecha, F. M. Sabatini, et al. 2022. "Citizen science plant observations encode global trait patterns." *Nature Ecology & Evolution* 6: 1850–1859. <https://doi.org/10.1038/s41559-022-01904-x>.
- Wolfe, B. E., V. L. Rodgers, K. A. Stinson, and A. Pringle. 2008. "The Invasive Plant *Alliaria petiolata* (Garlic Mustard) Inhibits Ectomycorrhizal Fungi in Its Introduced Range." *Journal of Ecology* 96, no. 4: 777–783. <https://doi.org/10.1111/j.1365-2745.2008.01389.x>.
- Wraith, J., and C. Pickering. 2017. "Tourism and Recreation a Global Threat to Orchids." *Biodiversity and Conservation* 26: 3407–3420. <https://doi.org/10.1007/s10531-017-1412-y>.
- Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428: 821. <https://doi.org/10.1038/nature02403>.
- Wyatt, J. L., and M. R. Silman. 2014. "Long-Term Effects of Clearcutting in the Southern Appalachians." In *The Herbaceous Layer in Forests of Eastern North America*, edited by F. Gilliam, 412–437. Oxford University Press.
- Yancy, A. J., B. R. Lee, S. E. Kuebbing, H. S. Neufeld, M. E. Spicer, and J. M. Heberling. 2024. "Evaluating the Definition and Distribution of

Spring Ephemeral Wildflowers in Eastern North America." *American Journal of Botany* 111: e16323. <https://doi.org/10.1002/ajb2.16323>.

Yin, Z., C. Zhang, X. Fan, N. Zhang, X. Zhao, and K. von Gadow. 2023. "Effects of Tree Density and Herbaceous Plants on Tree Seedling Survival Across the Growing and Non-Growing Season in a Temperate Forest." *Forest Ecology and Management* 545: 121234. <https://doi.org/10.1016/j.foreco.2023.121234>.

Yu, M., and O. J. Sun. 2013. "Effects of Forest Patch Type and Site on Herb-Layer Vegetation in a Temperate Forest Ecosystem." *Forest Ecology and Management* 300: 14–20. <https://doi.org/10.1016/j.foreco.2012.12.039>.

Zanne, A. E., D. C. Tank, W. K. Cornwell, et al. 2014. "Three Keys to the Radiation of Angiosperms Into Freezing Environments." *Nature* 506: 89–92. <https://doi.org/10.1038/nature12872>.

Zhukov, O., O. Kunah, Y. Dubinina, Y. Zhukova, and D. Ganzha. 2019. "The Effect of Soil on Spatial Variation of the Herbaceous Layer Modulated by Overstorey in an Eastern European Poplar-Willow Forest." *Ekológia (Bratislava)* 38: 253–272. <https://doi.org/10.2478/eko-2019-0020>.

Zobel, K., and J. Liira. 1997. "A Scale-Independent Approach to the Richness vs Biomass Relationship in Ground-Layer Plant Communities." *Oikos* 80: 325–332. <https://doi.org/10.2307/3546600>.

Zubek, S., K. Rožek, D. Chmolewska, et al. 2024. "Dominant Herbaceous Plants Contribute to the Spatial Heterogeneity of Beech and Riparian Forest Soils by Influencing Fungal and Bacterial Diversity." *Soil Biology and Biochemistry* 193: 109405. <https://doi.org/10.1016/j.soilbio.2024.109405>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Initial questions that resulted from the survey. **Appendix S2:** Conceptual diagram summarizing some of the key themes of the 100 questions about herbaceous plants in forest ecosystems.