Herbaceous plant diversity in forest ecosystems: patterns, mechanisms, and threats

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Abstract Studies conducted in forests have resulted in much of the ecological theory we build upon today. However, our basic understanding of forest ecology comes almost exclusively from the study of trees, even though they represent only a small fraction of the plant diversity present in forests. In recent decades there has been an increasing number of studies of forest herbs, broadening our understanding of plant community ecology in forest ecosystems. Here we highlight ten recent studies examining patterns and drivers of, as well as threats to, herbaceous plant diversity in forests. We first examine local, regional, and global patterns of herbaceous diversity in forests and how such patterns differ for woody versus herbaceous species. We then focus on ecological mechanisms that contribute to forest herb diversity, including the role of abiotic and biotic interactions. We end by discussing some major anthropogenic impacts on forest herb diversity,

identifying where herbs are particularly susceptible or particularly resilient to current and predicted changes in comparison to trees. The studies we feature demonstrate that patterns and drivers of diversity often differ between woody and herbaceous plant communities. To facilitate cross-site comparisons, there is great need for more standardized survey methods for herbaceous plants, for simultaneous measurements of multiple plant growth forms, and for incorporating herbs into long-term forest monitoring networks. In addition, the selected studies reveal how land-use history, overabundant herbivores, invasive species, and climate change are all impacting forest herb communities. Some common characteristics of herbaceous plants, such as limited dispersal and small stature, may make forest herb communities more susceptible to these anthropogenic impacts, while others (e.g., resprouting ability, clonal reproduction) may make them more resilient compared to forest trees. More research is needed from both plant ecologists and applied forest practitioners to predict how herbaceous forest diversity will change in the future.

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Introduction

In forest ecosystems large trees make up the bulk of living biomass, yet herbaceous plants are of critical importance to forest diversity, ecosystem processes, and conservation, despite their small stature (Gilliam 2014). In fact, in forests around the world, herbaceous plants are often the most species-rich of plant growth forms: they make up over 80% of all vascular plant species in temperate forests (Gilliam 2007; Spicer et al. 2020) and up to 45% in tropical forests (Linares-Palomino et al. 2009). This diverse group engages in a myriad of biotic interactions (Whigham 2004; Gilliam 2014) and can act as biotic filters to tree regeneration (Royo and Carson 2008). Forest herbs can serve as biodiversity indicators (Culmsee et al. 2014) and have been used as charismatic species of conservation concern (e.g., orchids) to galvanize public support for sustainable forest management (Swarts and Dixon 2009). Herbaceous plants are under increasing pressures resulting from anthropogenic activities; for example, climate change is leading to mismatches between herb phenology and the earlier onset of springtime and warmer temperatures (Heberling et al. 2019), as well as fewer pollination opportunities because of declining pollinator populations (Hanula et al. 2016). However, because forest ecologists have typically focused on trees, there is a relative paucity of research on the ecology of other plant growth forms, limiting our ability to understand and manage the threats to forest biodiversity as a whole. Here, we highlight recent studies on herbaceous forest plants, focusing on patterns of diversity at various scales, the underlying processes driving those patterns, and anthropogenic pressures threatening forest herb diversity. Rather than provide a synthetic review of the topic (e.g., Gilliam 2014), we select ten recent papers that are representative of some of the major themes and advances in the ecology of forest herb communities (Table 1), discuss their implications for the field, and suggest promising areas for future research.

Section 1: Patterns of forest herb diversity

Understanding where biological diversity occurs is both a central goal in ecology and the first step in designing effective strategies to sustain that biodiversity. Over the past several decades, the establishment and expansion of forest plot networks has greatly advanced our understanding of patterns of tree diversity in forest ecosystems around the world (e.g., ForestGeo, US FIA; Davies et al. 2021). By employing standardized methods, these plot networks foster cross-site comparisons of plant diversity. However, herbaceous plants are typically excluded from these networks, and individual herb studies use varying survey methods, precluding cross-site comparisons. Thus, compared to trees, much less is known about global patterns of sympatric herbaceous plant diversity in these forests. Cicuzza et al. (2013) partially filled this knowledge gap with their intercontinental comparison of tropical forest herb communities, which are particularly understudied (Massante et al. 2019). Using standardized sampling protocols at each forest site, the authors found similar levels of local herb species richness across the Americas, Africa, and Southeast Asia, although the continents were characterized by different herbaceous plant families and dominated by different taxonomic groups (e.g., dicot families were more dominant in American than African and Asian sites). Intriguingly, their analyses revealed some key differences between patterns of tropical herb and tree diversity as a function of the abiotic environment. Most notably, they found an increase in herb species richness with elevation, opposite to the decline in species richness with elevation typically reported for trees. While the general conclusions that can be drawn are limited by the small number of sites surveyed, this study underscores the need for standardized quantitative survey methods, as exist for woody plants in tree plot networks. Such standardized protocols would enable more robust cross-site comparisons of herbaceous plant diversity, provide insights into the extent to which herb assemblages are driven by current environmental heterogeneity versus evolutionary or biogeographic constraints, and foster a better understanding of differences in diversity patterns of different plant growth forms.

Vascular plant species span an amazing range of growth forms (and associated ecological strategies), from towering canopy trees to miniscule understory ephemerals. A fundamental question in plant ecology is how much do different plant growth forms contribute to diversity? This seemingly simple question has been difficult to answer, in part because few studies include all growth forms, all growth forms may not be present in many habitats, and the appropriate

Table 1 Table of selected focal papers, and contributions of each paper to our understanding of herbaceous understory diversity in forests

Citation	Topic	Contribution
Cicuzza et al. (2013)	Global patterns of herb diversity (patterns)	Quantified tropical understory herb richness across the globe, providing first standardized comparison across continents
Spicer et al. (2020)	Regional patterns of herb diversity (patterns)	Explicitly quantified contribution of herbs to plant species richness in comparison to other growth forms
Small and McCarthy (2003)	Local patterns of herb diversity (patterns)	Highlighted importance of conducting herb surveys at relevant spatial and temporal scales
Murphy et al. (2016)	Habitat filtering (processes)	Showed that habitat filtering was stronger for understory herbs than for woody seedlings in a tropical forest
Smith and Reynolds (2015)	Plant-soil feedbacks (processes)	Experimentally demonstrated that plant-soil feedbacks in temperate herbs vary among species and with light level
Warren and Bradford (2011)	Biotic interactions (processes)	Demonstrated the importance of biotic interactions, abiotic filtering, and dispersal limitation for temperate forest herb recruitment
Vellend (2004)	Land-use history (pressures)	Found that herb species and genetic diversity was higher in old-growth compared to secondary forest
Royo et al. (2010b)	Herbivory (pressures)	Illustrated the impact of overabundant deer on herb communities and the need for management strategies to overcome legacy effects
Merriam and Feil (2002)	Invasion (pressures)	Provided early evidence that non-native plant species can decrease forest herb diversity and abundance
Bertrand et al. (2016)	Climate change (pressures)	Showed that herbaceous community changes will lag behind climatic shifts, especially in warmer areas

scale of observation differs among growth forms (Fitzjohn et al. 2014). Moreover, there is inconsistency in definitions and treatment of forest herbs and the "herbaceous layer". Many authors include woody species < 1 m in height in surveys of the herb layer (e.g., "transient species" sensu Gilliam 2007; Gilliam 2014) and do not separate out plant growth forms, while others distinguish plant species based on woodiness, not stratum (e.g., Linares-Palomino et al. 2009). Studies that have estimated proportions of herbaceous versus woody species indicate great variability across biomes (Gentry and Dodson 1987a; Qian et al. 1998; Linares-Palomino et al. 2009), but explicit comparisons among ecosystems have been lacking. Spicer et al. (2020) addressed this knowledge gap in the Americas by comparing the proportion of species in each of the five major vascular plant growth forms (trees, shrubs, understory herbs, lianas, and epiphytes) in nine temperate and nine tropical forest sites. Confirming previous work in temperate forests (e.g., Gilliam 2007), they documented that herbaceous plant species make up the vast majority of temperate deciduous forests: 80% of all plant species in the nine

forests studied were terrestrial herbs, whereas only 7% of species were trees. In contrast, species richness was more evenly allocated among all growth forms in tropical forests. The study also illustrated an important structural difference between tropical and temperate forests: species in temperate forests were highly concentrated on the ground (< 2 m), while in tropical forests more diversity occurred higher up. Structurally dependent epiphytes (herbaceous and woody) and lianas together contributed 27% of tropical species, but < 3% of temperate species. These differences have important implications for fundamental ecological theory and biodiversity conservation. The authors called for a broadening of the scope of forest ecology and management to include herbaceous plants in both tropical and temperate ecosystems. The paper also raised the question of *why* latitudinal differences exist in relative species richness among plant growth forms. The tropical origin of many woody plant lineages may explain their higher diversity at lower latitudes (Massante et al. 2019), but other hypotheses such as a spring ephemeral niche for temperate herb diversity (Bratton 1976) and differences in biogeographic

history (e.g., Gentry and Dodson 1987b) remain largely untested.

Because herbaceous plants are smaller in stature and often have less-persistent aboveground structures than most woody plants, finer scale spatial and temporal variation in environmental conditions can strongly influence plant incidence and abundance, and hence measurements of diversity. Small and McCarthy (2003) tackled the practical methodological challenges this difference poses, using repeated surveys of a temperate forest to demonstrate variability in herb diversity and community composition across time and at several spatial scales. Even within a single forest, herb community composition and diversity varied significantly with location (e.g., between north- and south-facing slopes) as well as among different sampling periods. Further, depending on the spatial scale, different aspects of diversity were more or less apparent. For example, species richness was greater, but evenness lower, at larger sampling areas compared to smaller sampling areas. These results highlight the value of characterizing diversity in several ways to detect community change. A number of other studies have demonstrated the influence of topographic and edaphic variation on forest herb diversity (e.g., Murphy et al. 2016; Beck and Givnish 2021). Temporal variation in forest herb diversity, where the appearance of ephemeral taxa is linked to seasonal changes, has been well-documented in temperate forests (e.g., spring ephemerals; Bratton 1976) but less so in the tropics (e.g., in response to variation in seasonal rains). In moist tropical forests, structurally dependent forest herbs such as epiphytes are likely even more sensitive to small-scale environmental variability than terrestrial herbs due to stronger resource limitation, and face unique host-mediated habitat variation, such as branchfall, phenology, and bark characteristics (reviewed in Mendieta-Leiva and Zotz 2015). Although the patterns of diversity reported by Small and McCarthy (2003) are not surprising, their paper is an illustration of the importance of determining relevant temporal and spatial scales for studies of herbaceous plant diversity. The authors helpfully suggest baselines for sample size, sampling area, and timing for future surveys of herb communities. Their results also serve as a warning to researchers not to generalize too broadly from rapid snapshot approaches when studying forest herb communities.

Section 2: Processes driving and maintaining herb diversity

Determining how high levels of diversity are maintained in plant communities remains a fundamental challenge in community ecology. While forest ecologists have made considerable progress in this area (Nakashizuka 2001; Wright 2002), studies of the mechanisms that promote plant species coexistence and contribute to diversity maintenance in forests have largely been restricted to woody plants. Even among plants with different woody growth forms, the mechanisms that maintain diversity vary (Schnitzer 2018). At this point, few studies have tested the relative importance of resource niche partitioning, biotic interactions, disturbance, dispersal limitation, and other mechanisms in explaining species coexistence in terrestrial or epiphytic herb communities (but see Burton et al. 2011; Reich et al. 2012). Thus, we still do not know whether the same mechanisms maintain diversity of both woody and herbaceous communities in forests.

Abiotic niche partitioning, wherein local variation in abiotic resources and trade-offs among species life-history strategies promote high community diversity, is one of the best-established mechanisms driving species coexistence in woody plants (e.g., Denslow 1980; Silvertown 2004). The role of abiotic partitioning in shaping herbaceous communities, however, particularly in high-diversity tropical forests, is not well understood (but see temperate studies: Fahey and Puettmann 2007; Duguid et al. 2013; Kern et al. 2013). Murphy et al. (2016) provided much-needed data to narrow this knowledge gap, directly comparing tropical forest herb communities to woody growth forms in the understory (liana and tree seedlings). Their study highlighted two main differences in niche partitioning between herbaceous and woody plants. First, they found that habitat filtering was much stronger for herbaceous plants than for either tree or liana seedlings. Beta diversity, an indicator of spatial variation, was highest for herbaceous species, and habitat type explained over twice as much of the variance in herb community composition as compared to woody seedling communities. Second, Murphy et al. (2016) showed that patterns of woody and herbaceous diversity across sites were *not* correlated, suggesting different underlying processes among growth forms at the local scale. Abiotic drivers of

phylogenetic diversity may also differ between herbaceous and woody species. For example, along an elevation gradient in northeastern China, Qian et al. (1998) showed that climate and soil characteristics explained very little variation in phylogenetic alpha diversity of herbs but the majority of variation in woody plants. Further comparative studies are clearly needed to determine the relative effects of ontogenic stage, abiotic conditions, and spatial scale on patterns of woody versus herbaceous plant diversity.

In addition to the abiotic environment, biotic interactions drive patterns of plant distribution and diversity. It is well-established that species-specific enemies such as herbivores and pathogens drive density-dependent mortality of tree seedlings, potentially contributing to the maintenance of tree diversity (e.g., Bagchi et al. 2014; Comita et al. 2014). In particular, the importance of soil microbial communities in mediating plant–soil interactions and subsequent fitness consequences has become more apparent in the past few decades (e.g., Mangan et al. 2010; Van der Putten et al. 2013). However, little is known about the effects of plant–soil feedback on the structure of forest herb communities. Smith and Reynolds (2015) provided some of the first empirical evidence for plant–soil feedback in native forest herb communities. They compared the performance of six understory species (two grasses, two forbs, one shrub, and one invasive liana) in their own soil against soils conditioned by each of the other competitors, at three different light levels in a full-factorial experimental design. As expected, the authors found evidence for strong negative feedbacks, suggesting that plant–soil feedbacks may contribute to coexistence of these plant species. However, these feedbacks were only negative in three of the four herbs and only at high light levels (23–50% full sun), suggesting that they may have less of an effect on herb species coexistence than other factors in the deeply shaded conditions in which understory herbs usually grow. Interestingly, this finding contrasts with results from studies of tropical and temperate tree seedlings that found stronger pathogen impacts and more negative plant–soil feedbacks under low, rather than high, light conditions (Augspurger and Kelly 1984; McCarthy-Neumann and Ibáñez 2013). The one herbaceous species that showed neutral to positive plant–soil feedback at all light levels, *Asarum canadense* (Aristolochiaceae), exhibits clonal growth and can form dense

monocultural patches in mature forests, traits that are characteristic of many understory herb species (Whigham 2004). Future work on herbaceous plant–soil feedback could use a trait-based approach to extend these species-specific responses to whole herb communities (Van der Putten et al. 2013). The results of Smith & Reynolds' research, and complementary studies focused on plant–soil feedback among native and non-native species (e.g., Hale et al. 2016), suggest that plant–soil feedbacks also mediate the invasion of forest herb communities by non-native species (see section below on threats to herb diversity).

The outcome of biotic interactions, including interactions between plants and their natural enemies, is often dependent on local abiotic conditions. Warren and Bradford (2011) combined experimental and observational data to document how the effect of fungal pathogens on recruitment and survival of two temperate herb species depended on soil moisture. They showed that both herb species, when transplanted as adults, survived best at soil moisture levels much higher than at soil moisture levels corresponding to where their natural populations peaked. However, the recruitment success of transplanted seeds in these high-soil-moisture sites depended on the addition of fungicide. At high moisture levels, seed germination rate was two to three times higher with fungicide than without, suggesting that a strong fungi-mediated bottleneck explains why adult populations do not peak at their physiologically ideal soil moisture level. These results clearly indicate that biotic interactions can and do limit the distribution of herbaceous species, resulting in a realized niche that is narrower than the availability of environmentally suitable sites. Moreover, the study showed that the two herbs' susceptibility to pathogens differed throughout ontogeny: as in trees, earlier life stages were more vulnerable than adults (e.g., Gilbert et al. 1994). In a complementary experiment, Warren et al. (2010) demonstrated that dispersal of seeds by ants also decreased as soil moisture increased, dropping off to approximately zero at moisture levels where adult plants still had high population densities in the wild. Compared to woody plants, herbs typically have exceedingly short dispersal distances (Cain et al. 1998; but see Myers et al. 2004). Therefore, both dispersal limitation and biotically mediated recruitment success may contribute more to patterns of herb distribution and composition than in woody species (Ehrlén and Eriksson 2000;

Gilbert and Lechowicz 2004). However, comparatively little data exists on abiotic and biotic factors that influence herbaceous species in tropical forests. Studies that simultaneously assess the relative contributions of abiotic and biotic drivers to the composition, structure, and distribution of tropical forest herb communities will rapidly advance our understanding of the ecology and evolution of both herbaceous and woody plant diversity (e.g., Lagomarsino et al. 2016).

Section 3: anthropogenic pressures on herb diversity

Humans have been reorganizing natural plant communities for millennia, both increasing and decreasing plant diversity across landscapes (Flinn and Vellend 2005; Maezumi et al. 2018). However, in the last few centuries, the direct and indirect effects of anthropogenic activities have become the dominant driving force behind community turnover, population decline, and increased extinction risk in forests (e.g., Ellis et al. 2012). Herbaceous communities often appear to have different, and at times opposing, responses to human disturbance in comparison to trees, but the consequences of anthropogenic pressures on herb diversity are still poorly understood (Decocq et al. 2014). Here, we focus on four of the main chronic and acute threats to herbaceous plant diversity in forest ecosystems: land-use legacies, overabundant herbivores, invasive species, and climate change. This list is not exhaustive; we note that a growing literature on herbaceous responses to forest management issues such as logging, fire regimes, and nutrient deposition are worth future in-depth review (outlined in Gilliam 2007, 2014). Moreover, some anthropogenic pressures, such as forest harvesting, are well studied in temperate forests (see Duguid and Ashton 2013) but less so in tropical ones (but see, e.g., Castro-Luna et al. 2011).

Forest conversion, in particular for agriculture, causes drastic and long-term shifts in plant communities, including declines in the species and functional diversity of herbs (e.g., Singleton et al. 2001; Dupouey et al. 2002; Sonnier et al. 2014). Vellend's (2004) study contributed to our understanding of the impacts of land-use history on forest herbs, focusing on how both genetic and species diversities differ between secondary (post-agricultural) and uncleared forests. Pairing herb community surveys with analysis of three molecular markers in *Trillium grandiflorum*

(Melanthiaceae), Vellend (2004) found lower species diversity and lower genetic diversity in post-agricultural forests compared to undisturbed forests. In fact, land-use history was the only significant predictor of all diversity metrics and explained approximately 40% of the variability in both species evenness and genetic divergence. These results have implications for herb population and community stability following human disturbance. Although forests that regenerate following agricultural abandonment do recover some measure of their species diversity (e.g., Singleton et al. 2001), genetic diversity is also necessary to ensure sustained reproductive success and resilience (Vellend and Geber 2005). Bottlenecks or founder events may be an important cause of genetic drift in fragmented forest herb populations, especially when populations are small and/or isolated (Chung et al. 2020). Because of their shorter mean dispersal distances in comparison to trees (Cain et al. 1998; but see Myers et al. 2004), herbs may have reduced colonization ability and be more susceptible to declines in genetic diversity, especially in forest fragments. These processes could also be occurring at the community level, wherein only a subset of species can successfully disperse to and establish in secondary forests. More studies that explicitly compare diversity at multiple levels are needed to generalize which processes determine species versus genetic diversity (Vellend and Geber 2005). These data are necessary to predict where drift, migration, and selection will lead to local extinctions in the future.

In most forested landscapes throughout the world, activities associated with human settlement have also systematically removed apex predators and improved conditions for a few large herbivores, causing biodiversity loss and other dramatic shifts in plant communities (Ramirez et al. 2018). The problem of overabundant white-tailed deer in the U.S. eastern deciduous forest biome illustrates the complexity of managing forests for biodiversity in this context. An important lesson comes from Royo et al. (2010b) and similar studies (e.g., Krueger and Peterson 2009; Nuttle et al. 2014) that explicitly compare the responses of herbaceous and woody plants to deer. Their results illustrate the myriad direct and indirect effects of elevated deer densities on understory plant diversity and emphasize the need for management strategies that go beyond simply reducing deer populations. Culling deer improved the performance

metrics of three deer-sensitive herbaceous indicator species at the individual plant and population level, but these benefits did not translate to the community level (Royo et al. 2010b). Indeed, although browse impact decreased to historic levels across a landscape after culling, neither species richness nor evenness of woody and herbaceous species had increased four years post-cull. Both the indirect and legacy effects of deer, such as increased seed predation by small mammals, dense stands of deer-resistant ferns that inhibit recruitment of other plants, and altered seed dispersal networks, likely contributed to the continued failure of new species to recruit into plots (Côté et al. 2004). Subsequent studies have shown that these legacy effects can last decades (e.g., Nuttle et al. 2014). These studies also demonstrate how empirical research can inform management strategies; notably, they suggest that reducing deer populations as well as interventions that promote the recruitment of both herb and tree seedlings (e.g., creation of light gaps) are needed to address biodiversity loss (e.g., Royo et al. 2010a). Combination management techniques are particularly essential for the recovery of native herb species because unlike trees, herbs cannot grow above the browse line to escape ungulate herbivory pressure. Herbs are also unlikely to independently re-seed areas protected from deer due to their shorter seed dispersal distances. The conservation of herbaceous plant diversity can be complementary to the management of tree or animal populations in tropical forests as well. For example, sustainable agroforestry systems can provide habitat for epiphytes and understory herbs (e.g., Rossi et al. 2011), which in turn can support diverse faunal communities and provide ecosystem services (e.g., Cruz-Angón and Greenberg 2005).

Invasion by non-native species—plant competitors, animals, and pathogens alike—poses another major threat to herbaceous plant communities in forests across the world, in particular within fragmented or degraded forests (Gilliam 2007; Bellard et al. 2016). One of the first papers to explicitly test the effects of non-native species on native forest herb communities was Merriam and Feil (2002). They found 41% fewer herbaceous species and 75% fewer individual herb stems in a 75–100-yr-old secondary mixed-hardwood forest with nearly 100% understory cover of the non-native invasive shrub privet (*Ligustrum sinense*, Oleaceae) compared to adjacent reference forest with little invasion. Removal of the invasive privet reduced the difference in herb species richness and equalized herbaceous stem counts between invaded and uninvaded forests after six months. Subsequent studies have found similar negative correlations among non-native species abundance and herbaceous diversity at small scales (e.g., Hale et al. 2006), and a few have demonstrated that the removal of invasive species increased cover, survival, and/or performance of native herbs (e.g., Prasad 2010). However, additional research is needed to improve understanding of the mechanisms behind non-native species invasions, as well as our ability to predict both the colonizing ability of incoming species and the susceptibility of invaded habitats. Propagule pressure (Von Holle and Simberloff 2005), disruption of belowground mutualisms (Hale et al. 2016), and concurrent multi-species invasions (Kuebbing et al. 2013) all seem to reduce the extent to which diverse forest herb communities persist when invasive species are introduced. Overabundant herbivores (Eschtruth and Battles 2009) and land-use history (Mullah et al. 2014) can further mediate the impacts of invasive species on understory forest diversity. Understanding invasibility, resistance, and the role of propagule pressure is particularly important for understory herbs, because a majority of plant invaders are herbaceous (Rejmánek and Richardson 1996), and therefore intrinsically present strong resource and niche space competition to native herbs. The extent to which herbaceous forest communities are resistant to invasive species is currently not well understood.

Finally, the various impacts of human-induced climate change interact with all of the more direct anthropogenic pressures mentioned above. Major shifts in herb distributions, population declines, and some extinctions are expected in response to climatic warming (Skov and Svenning 2004; Bellemare and Moeller 2014). Temperate forest herbs and tropical montane epiphytes may be particularly vulnerable, because of their narrow habitat ranges and limited ability to disperse quickly enough to track changing climatic conditions (Nadkarni and Solano 2002; Bellemare and Moeller 2014). Other authors are more optimistic. Herbs are thought to evolve faster than woody plants (Smith and Donoghue 2008), occupy a larger climatic niche (Smith and Beaulieu 2009), and may be buffered by the forest overstory (Landuyt et al. 2019), potentially enabling species to adapt to or escape from changing climates. In either case, many

organisms are resilient to predictable and short-term environmental changes that occur naturally and may not respond immediately to the unprecedented and prolonged climate forcing that is occurring (Corlett and Westcott 2013). These potential lags in the response to observed changes in climate—or "climatic debt"—are important to understand if we are to predict future community structure and function. Bertrand et al. (2016) explored the determinants of climatic debt and tested whether forest herb assemblages in France could keep pace with local warming. Their study calculated the climate debt by comparing the measured local temperature with "optimal" temperature inferred from the local assemblage of herbaceous taxa present at the time. The authors found that plant assemblages in areas with warmer baseline temperatures had a much greater climate debt, and therefore greater mismatch, than communities in areas with cooler baseline temperatures. Bertrand et al. (2016) suggest that phenotypic plasticity and evolutionary adaptation will ultimately be unable to deal with faster temperature changes, in contrast to Smith and Donoghue (2008) and Smith and Beaulieu (2009). Forest herbs will likely respond to climate at the community level, with shifts in species composition driven by increases in species previously found in hotter and drier sites and declines of heat- and drought-sensitive species (e.g., Harrison et al. 2010). Similar climate-driven shifts in community composition have been reported for forest trees, as well as for plant communities in other ecosystems (Feeley et al. 2020). Future models should incorporate the effects of increased extreme weather events and variability (e.g., Hsu et al. 2018; Kennard et al. 2020) and potential positive feedback from climate-induced overstory decline (e.g., Zellweger et al. 2020), as well as more information on intraspecific variation in traits (e.g., specific leaf area) that could contribute to the adaptation of herbaceous plant communities to global change (Blondeel et al. 2020).

Conclusion

Several themes emerged from our focus on a few recent studies of forest herb diversity. First, to fully understand the diversity and distribution of herbaceous plants in and across forests at multiple spatial and temporal scales, the field will need to resolve several methodological challenges of surveying herbs. While recent global and regional studies have amassed impressive databases of species lists, standardizing surveying methods, incorporating herbs into existing long-term research sites, scaling surveys to balance feasibility and small-scale variation, and increasing support and training for herbaceous botanical experts are all essential for making further progress in understanding the distribution and success (i.e., abundance) of herbs in forest ecosystems (Crisci et al. 2020). Our review concentrated predominantly on species-level measures of diversity, but future studies should encompass phylogenetic (Massante et al. 2019), genetic (Vellend 2004), and intraspecific phenotypic variation (Blondeel et al. 2020). Analyses of forest herb functional traits will also be an important tool to test which trade-offs shape herbaceous community composition and diversity (e.g., Burton et al. 2020; Rundel et al. 2020) and mediate responses to anthropogenic disturbance (Curzon et al. 2020).

Second, direct comparisons of various growth forms are necessary. As illustrated by several of the studies highlighted above, the patterns and drivers of woody plant diversity cannot be extrapolated to herbaceous communities. Habitat filtering appears to be a stronger driver of herb diversity than woody diversity (Murphy et al. 2016), but dispersal limitation and biotic interactions can strongly limit realized niche space for herbaceous species (Warren and Bradford 2011). Further, although we know that plant–soil feedbacks vary among herbaceous species and across abiotic gradients, similar to patterns found in tropical trees (Smith and Reynolds 2015), the extent to which plant–soil feedbacks and other biotic interactions contribute to forest herb species coexistence is largely unknown.

Finally, certain characteristic traits of herbs, such as short-distance seed dispersal, have implications for both patterns of diversity and the responses of herbaceous communities to anthropogenic disturbance (Klimešová et al. 2016). Due to their limited dispersal, diverse herbaceous communities may be particularly slow to re-assemble in heavily disturbed habitats without intact local populations and are unlikely to migrate quickly enough to track optimal conditions under climate change (Bertrand et al. 2016). Forest management plans, therefore, may need to consider more active restoration strategies to promote diverse herbaceous understories. On the other hand, herbs that

have a seed bank, long-lived underground propagules, disturbance-adapted dispersers (e.g., deer), or organs that can quickly recover from aboveground disturbances (Haukioja and Koricheva 2000) may be even more resilient than woody species to the predicted increase in extreme natural disturbances associated with climatic change or to forest management practices such as logging or understory burning. Unfortunately, many of the anthropogenic pressures we highlight here, as well as additional pressures (e.g. fire, nutrient deposition, logging), are acting simultaneously and at multiple spatial scales. To predict the structure and function of herbaceous plant communities of the future, we need long-term studies that integrate data on multiple aspects, including abiotic and biotic neighborhoods, anthropogenic disturbances and land-use histories, as well as past, present, and future climate scenarios at spatial scales that are relevant to herb populations (e.g., Freckleton et al. 2011; Tuomisto et al. 2019).

Data Availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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