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RESEARCH ARTICLE

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Evaluating the definition and distribution of spring ephemeral wildflowers in eastern North America

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Abstract

Premise: The herbaceous layer accounts for the majority of plant biodiversity in eastern North American forests, encompassing substantial variation in life history strategy and function. One group of early-season herbaceous understory species, colloquially referred to as spring ephemeral wildflowers, are ecologically and culturally important, but little is known about the prevalence and biogeographic patterns of the spring ephemeral strategy.

Methods: We used observations collected by the Global Biodiversity Information Facility (GBIF) to quantify the ephemerality of 559 understory forb species across eastern North America and classify them according to a continuous ephemerality index (ranging from 0 = never ephemeral to 1 = always ephemeral). We then used this information to model where ephemeral forbs were most common across the landscape with the goal of identifying geographic and environmental drivers important to their distributions and ranges.

Results: Only 3.4% of all understory wildflower species were spring ephemerals in all parts of their range, and 18.4% (103 species) were ephemeral in at least part of their range. Spring ephemerals peaked in absolute species richness and relative proportion at mid latitudes.

Conclusions: Spring ephemeral phenology is an important shade-avoidance strategy for a large segment of the total understory species in temperate deciduous forests. In North America, the strategy is relatively most important for forest understories at mid latitudes. The definitions of spring ephemerality we provide here serve as an important ecological context for conservation priorities and to evaluate responses of this biodiverse group to future environmental change.

KEYWORDS

biodiversity, biogeography, community science, ephemerality index (EI), latitudinal gradients, phenological strategy, temperate forest

Understory herbaceous species make up approximately 80% of the total plant species in eastern North American temperate deciduous forests (Gilliam, 2007; Spicer et al., 2020). They provide important ecosystem services including early-season floral resources and soil nutrient cycling (Muller and Bormann, 1976; Gilliam, 2007). A subset of these species, commonly referred to as spring ephemeral wildflowers, are only active in spring, relying solely on elevated light availability (when canopy trees are leafless) to facilitate their annual energy budgets (Uemura, 1994; Neufeld and Young, 2014). The duration of favorable growing conditions before tree canopy closure decreases with increasing latitude (Neufeld and Young, 2014), suggesting that spring ephemeral diversity could also decline with increasing latitude (Routhier and Lapointe, 2002). However, despite the relative importance of spring ephemeral wildflowers to North American biodiversity, a quantitative definition of what constitutes a spring ephemeral wildflower is still missing from the literature, making it difficult to evaluate this hypothesis in a meaningful way.

Light availability is a critical limiting resource for understory plants in closed-canopy forests. Understory light levels in temperate deciduous forests are dependent on canopy openness (e.g., the proportion of light intercepted by canopy tree leaves) and on canopy tree phenology (i.e., the timing and duration of when canopy trees have leaves). The amount of light reaching the forest floor decreases with increasing canopy leaf area index and varies with cyclical annual "phenoseasons" in temperate deciduous forests (Hutchison and Matt, 1977), the dominant forest type across eastern North America. This variability includes the availability of sunflecks, which are more abundant before full canopy leaf expansion, but can provide critical light to summer-green and evergreen understory plant species (Way and Pearcy, 2012). Understory light availability is also dependent on latitude and local geography, especially in spring when the sun's zenith is lower in the sky than it is in summer, particularly in poleward locations (Neufeld and Young, 2014). In these systems, light is therefore most limiting starting with the onset of canopy leaf out in late spring, lasting through the summer until canopy leaf senescence in autumn as the trees return to dormancy for the winter. As a result, understory plant species have adapted a wide variety of different strategies to survive and persist in such a highly variable environment.

Forest understory plants must either be able to tolerate or avoid shade to assimilate enough carbon from photosynthesis for survival, reproduction, and growth of new tissue (Hull, 2002; Valladares and Niinemets, 2008). Shade tolerators, such as most summer-blooming wildflowers (sensu Neufeld and Young, 2014), employ a photosynthetic strategy that allows them to efficiently photosynthesize under reduced light levels, albeit with limited capacity to capitalize on high light (Hull, 2002; Valladares and Niinemets, 2008). In contrast, shade avoiders typically maintain high maximum photosynthetic rates while altering their growing season activity to maximize their access to high light (Lapointe, 2001), thereby reducing or eliminating their need for better efficiency in shady conditions. Importantly, temperate understory plant species commonly employ some combination of both strategies by maximizing photosynthetic rates in early spring and then downregulating their photosynthetic machinery once the canopy closes (Rothstein and Zak, 2001; Bauerle et al., 2012; Peltier and Ibáñez, 2015; Heberling et al., 2019a).

Many shade avoiders in temperate deciduous forests fall into the category of spring ephemeral, meaning that they rely solely on access to spring light to assimilate carbon before retreating to belowground dormancy as the canopy closes (Neufeld and Young, 2014). Most of these species create large belowground rooting structures to store carbon (Lubbers and Lechowicz, 1989; Lapointe and Lerat, 2006; Gandin et al., 2011). These storage structures facilitate summer dormancy and belowground growth during the autumn and winter until emergence the following spring (Lapointe and Lerat, 2006). Access to spring light is important for the carbon budgets of all spring-active plants (Heberling et al., 2019b; Lee and Ibáñez, 2021a, b), but spring carbon gain represents 100% of the carbon assimilated by spring ephemerals each year.

The term spring ephemeral is commonly used in botanical literature, yet there is no consensus about the timing cut off for whether an individual species is "ephemeral" or not. Some authors use a strict definition of ephemerality that only includes plants that complete all aboveground activity, including leafing, flowering, fruiting, and senescence, before full canopy closure (Lapointe, 2001; Neufeld and Young, 2014; Lee et al., 2024b). We employ this definition here. Other authors use a more relaxed definition to include any spring blooming species that has finished flowering before canopy closure regardless of whether a given species continues to photosynthesize for weeks or months after canopy closure (Lubbers and Lechowicz, 1989; Irwin, 2001; Constable et al., 2007). Although one possibility for this inconsistency is a lack of strict definitions for this life history strategy, it is also possible that some species might differ in their ephemerality over the extent of their range because of phenotypic plasticity, ecotypic variation, or complex interactions with local environmental cues.

Regardless of definition, as far as we know, all of the scientific literature defines species-level ephemerality as binary—either species are ephemeral or they are not. The possibility that species differ in the degree of their ephemerality across their range is supported by evidence showing different phenological sensitivities (i.e., the magnitude of change in phenology over variation in a driver, such as spring temperature over time) for this group of species across large geographical gradients (Alecrim et al., 2022; Miller et al., 2022) and at smaller scales with local, natural variations in canopy closure (Dion et al., 2017). Specifically, Miller et al. (2022) and Alecrim et al. (2022) found that overstory–understory asynchronization depended on what part of the deciduous biome was considered (northern, central, or southern), although recent evidence suggests that these patterns may be substantially affected by the source of data used in analysis (Lee et al., 2024a). Dion et al. (2017) found that *Allium tricoccum*, a spring-active wildflower, delayed leaf senescence under tree canopies with later leaf-out phenology, compared to those under canopies with earlier closure, resulting in higher biological success. Combined, these findings suggest that plants have adapted with a different responsiveness to environmental cues in different parts of their ranges, which could theoretically lead to differences in overall phenological strategy. Additionally, forests located within the ice margin of the last glacial maximum underwent geographic displacement (Dyer, 2006), and species migrated northward at different rates and paths following glacial retreat utilizing a variety of different dispersal mechanisms (Cain et al., 1998; Vellend et al., 2003). This post-glacial dispersal shaped the community composition and structure of these forests, and likely influenced species-level phenological sensitivities across the landscape. These large-scale questions are becoming more readily testable with the emerging tools of "macrophenology" (sensu Gallinat et al., 2021), including the application of remote sensing and community science data sets.

Using this strict definition of spring ephemeral wildflowers, we combined remote-sensed imagery and observational phenology with data from herbarium collections aggregated from the Global Biodiversity Information Facility (GBIF) to estimate spring ephemerality in forest herbaceous understory plants across eastern North America. Our goals were to (1) develop a new, continuous metric of spring ephemerality allowing for spatial variation in ephemerality across species ranges and (2) apply this new metric to quantify how spring ephemeral species richness varies across the landscape.

MATERIALS AND METHODS

We divided our analysis into two parts, consistent with the goals described above. To meet Goal 1, we combined regional species checklists with observations of plant activity aggregated from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/; accessed 12–13 March 2023) and remote-sensed MODIS green-up data to define spring ephemerality by species and region (i.e., grid cell, described below). To meet Goal 2, we used this information to explore the geographic distribution of the spring ephemeral strategy.

Goal 1: Defining spring ephemerality

Species selection

To meet our first goal, we acquired 16 site-level floristic species checklists collected in forested natural areas across eastern North America that provide representative lists of regional species pools (Appendix S1: Table S1, Figure 1A). Species lists were distributed across the eastern North American deciduous forest biome with sites from as far south as Congaree National Park in South Carolina, northwest as far as Huron Mountain Club on the upper peninsula of Michigan, and as far northeast as Laurence Mauricie National Park in Quebec. A full list of site names, abbreviations, and reference citations is in Appendix S1 (Table S1). We consolidated the site-level lists into a combined species list incorporating all species from all sites ($N = 1666$ species) and used the USDA PLANTS Database (https://plants.usda.gov/home) to identify each species' taxonomy and growth habit. We retained all forb species (herbaceous vascular species excluding woody plants, grasses, sedges, and ferns), resulting in 834 species encompassing 81 taxonomic families and 329 genera. We then excluded non-forest species based on published habitat descriptions (Weakley, 2024), aggregated cultivars and subspecies to the species level, and updated species names to account for synonymy using the R package taxize (Chamberlain and Szöcs, 2013). We removed species that did not have enough GBIF observations for a full statistical analysis (i.e., fewer than 10 observations per grid cell, see below), resulting in a final species list of 559 species (see Appendix S2 and Data Availability Statement).

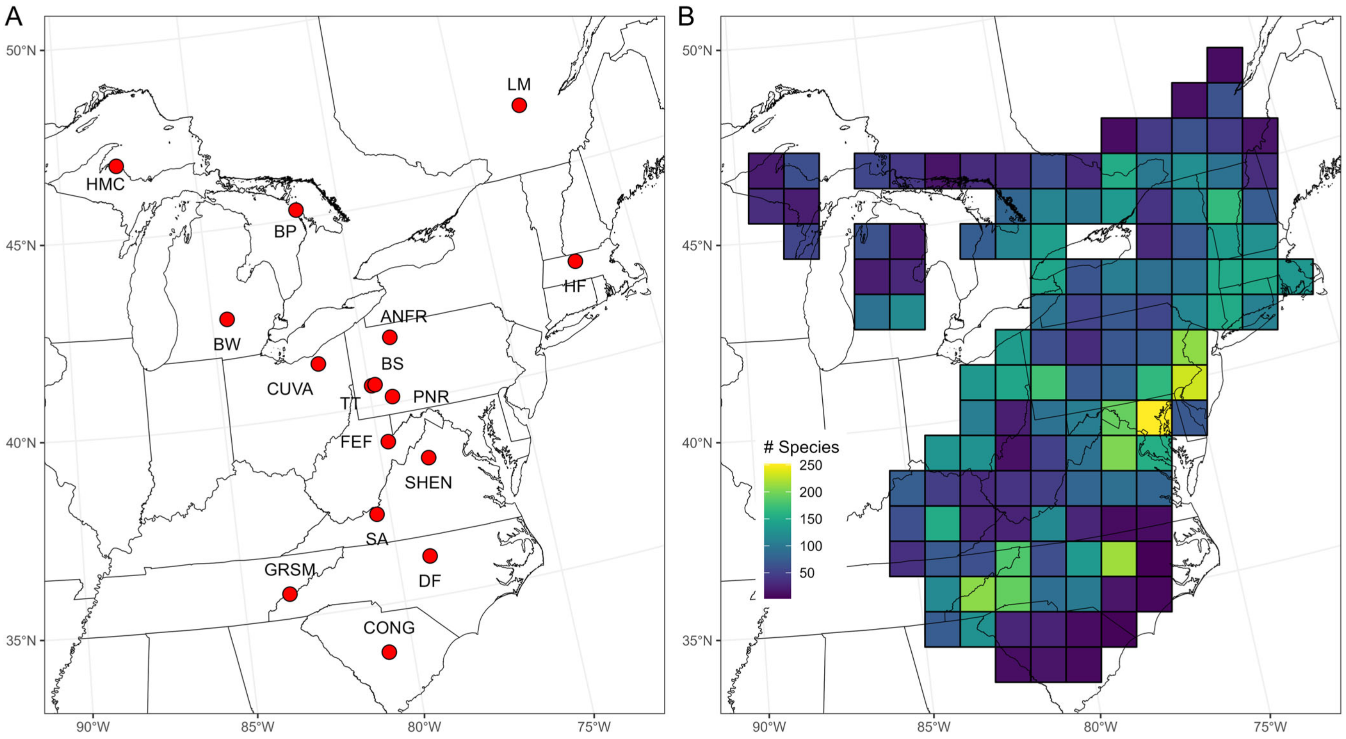

FIGURE 1 (A) Map of the 16 sites for which species lists were used to compile the comprehensive species list used in this study. Site abbreviations and descriptions of site-level species lists can be found in Appendix S1 (Table S1). (B) Map of the 128 equal-area grid cells used to extract GBIF observations of plant activity, remote-sensed green up and environmental data. Cell color indicates the estimated number (#) of understory plant species in each cell.

Data processing

To define spring ephemerality, we needed information about (1) the phenology of the understory plants in our species list and (2) the relative timing of tree canopy closure for each of the 16 sites. For the phenology information, we followed the general approach described by Belitz et al. (2023), where we created an equal area grid consisting of 100 × 100 km grid cells with which to extract phenological observations and evaluate ecological variation. First, we extracted all research-grade species observations between 2015–2021 from GBIF (data downloaded 12–13 March 2023) using the R package rgbif (Chamberlain et al., 2023; filtered list of observations available at https://doi.org/10.15468/dd.zyywht). Observations from GBIF were primarily composed of community-science data (Appendix S1: Figure S1; 98.5% of total observations). The majority of these observations were collected by users of iNaturalist (https://www.inaturalist.org/; 86.7% of total observations; see Appendix S2 for a full list of data sources), a community-science platform where users upload images of plants, animals, and other biota along with metadata about where and when the image was collected. With the help of artificial intelligence software and an extensive user-base, users also identify each organism to species where possible, with "research-grade" observations being those for which more than two-thirds of identifiers agree on a taxon. For species that did not return any observations from the GBIF search, we extracted observations directly from iNaturalist using the R package rinat (Barve and Hart, 2022). For each species, we removed duplicate observations (same species observed in the same location on the same day and by the same user) to avoid pseudoreplication of observations, and we removed all observations assigned to the first of a month due to a previously described artifact where observations that are missing exact day data are occasionally automatically and erroneously assigned to the first of the month (Belitz et al., 2023). We assumed that all observations in our database were of living, active plants (as opposed to senesced plants).

To assess whether spring ephemerality within a given species varies across space, we constructed a grid across eastern North America consisting of equal-area 100 km × 100 km grid cells bounded by 25° to 47.88°N and −97.00° to −52.02°W for an initial total of 1089 cells that encompassed all 16 sites where species lists were compiled. We then collated species-level observations in each cell using location data accompanying each observation and removed cells with no observations (e.g., those in the middle of the Atlantic Ocean). Previous research has shown that estimates of activity period or growing season length can be strongly biased by the number of observations used to make the estimations (Pearse et al., 2017; Belitz et al., 2020b). Specifically, estimates of active periods are more accurate when they are based on more observations. However, observation-based biases have been documented in iNaturalist and other crowd-sourced data sets (Belitz et al., 2020b), such as higher observer effort in populated areas. As such, we adopted criteria that are considered best practice for assessing spatial variation in phenological activity (Belitz et al., 2023). Namely, we only considered a species within a given grid cell if there were more than 10 recorded observations of that species in that cell in our data set, a threshold that was previously shown to allow accurate estimation of active period duration (Belitz et al., 2020b). Further, we used the R package phenesse (Belitz et al., 2020a) to estimate the 99th percentile of activity period for each species and grid cell, a measure considered to be equivalent to the end of the observed active period (Belitz et al., 2020b), therefore representing an estimate of early summer senescence in spring ephemeral wildflowers.

For each species in a given cell, regardless of the number of observations, we estimated activity periods from 500 iterations of bootstrapped, randomized distributions of observational data. In short, this approach (detailed fully by Belitz et al., 2020b) allowed us to statistically account for differences in observation effort that might otherwise skew our estimates of active season length. We chose the 99th percentile estimator in this analysis because it was the most conservative of all thresholds that we considered (95th and 99th percentiles of raw data and 95th and 99th percentiles of the phenesse results; Appendix S1: Figure S2). Furthermore, although threshold choice changed species-level estimates of ephemerality index, it did not significantly affect the overall signal in our final analysis (Appendix S1: Figure S2), indicating that the modeling approach was robust to this choice in statistical approximation.

Next, to ensure that the species in our combined list were representative of the geographic scope of grid cells used in analysis, we narrowed the cells used by removing those that were further than 100 km from one of the 16 sites with species lists and that were not between any two sites. We further removed grid cells if over half of their area was covered by water (primarily associated with cells in the Great Lakes and coastal Atlantic Ocean regions), or if estimates of canopy closure were overly biased by agricultural green-up (primarily associated with the Midwest region in the Unites States and the Ontario Peninsula in Canada; see next paragraph). Figure S2 (Appendix S1) provides a graphical depiction of which of the original 1089 cells were or were not included and the reasoning for excluding cells from the broader analysis. Cumulatively, this grid cell thinning resulted in a working data set comprising 642,526 observations of 559 forest understory forb species from 128 grid cells (100 × 100 km) from northern Georgia to northern Wisconsin and southern Quebec (Figure 1B).

Lastly, because our definition of spring ephemerality depends on the phenology of both the understory forbs and overstory canopy trees, we estimated cell-level canopy close phenology using MCD12Q2 enhanced vegetation index (EVI) based on green-up data collected by MODIS (Gray et al., 2019). Specifically, we extracted the "maturity" parameter, which corresponds to the day of the year when a pixel (250 km^2 spatial resolution) reaches 90% of its peak green-up value each year. This metric has high fidelity to ground-truthed measures of canopy development and start of spring (Peng et al., 2017) and should be interpreted as a relatively conservative proxy for the beginning of the summer shady period in deciduous forests. We averaged 250 km^2 pixel EVI values within each 100 × 100 km grid cell across the same years used to collate GBIF observations (2015–2021), excluding pixels associated with impervious surfaces and water cover. We then estimated the day of the year of canopy closure as the median pixel value within each grid cell. As described above, we removed any cells where canopy closure was estimated to occur after day 181 (~1 July), which indicated a strong skew from agricultural green-up associated with summer crops like corn and soybean (e.g., Wardlow et al., 2007) in August and September (Appendix S1: Figure S3).

Quantifying ephemerality

Using the combined grid cell-level understory herbaceous phenology and estimated canopy close information, we designated every species in every cell where it was observed as either "spring ephemeral" or not, with ephemerals defined as species that were only active (i.e., the 99th percentile estimate of the end of activity period) before the estimated day of canopy close from our MODIS data. Importantly, this classification system allowed species to be considered ephemeral in some cells while not being considered ephemeral in others (e.g., a species could have the same temporal distribution of observations in all cells where it occurs, but the ephemerality designation could differ because of variation in the cell-level estimates of the day of canopy closure in that year). Species were thus assigned an overall ephemerality index (EI) value, calculated as the proportion of cells where it was designated ephemeral divided by the total number of cells in which it was observed. For example, a species defined as ephemeral in 36 of the 67 cells it was observed in would have an EI value of 0.54. Species that were ephemeral in every cell in which they are observed would have an EI of 1, while those that were never considered ephemeral in any cell would have an EI of 0.

Following the assignment of EI values, we looked for species with categorizations that were likely erroneous, such as for those that we knew had an evergreen or semi-evergreen leaf habit but returned an EI value > 0. We also removed two *Allium* species that, although their photosynthetic strategies are typically in line with the spring ephemeral strategy, both species fruit well into the summer shady period and therefore do not meet our strict definition of ephemerality used in this analysis (even though leaves may senesce in spring). For each species with 0 > EI > 1, we surveyed the primary literature and field guides describing its leaf habit and, if it was described as being evergreen or semi-evergreen, we manually changed its EI to 0; the EI of 25 species was thus converted to 0 (Appendix S1: Table S2). Figure S4 (Appendix S1) depicts the relationships between estimated canopy close and estimated species-level end of season timing, specifically highlighting the 25 species that were misclassified according to our data set. Importantly, we did not alter EI values for species described by field guides as deciduous, leaving open the possibility that, although we would not consider a species to be ephemeral based on our personal observations/experience, it is possible that ephemerality varies across space and that the EI metric is picking up on true biogeographical variation in this trait. A comprehensive list of species and their EI values is provided in Appendix S2.

Assumptions for the index

Importantly, to conduct this analysis, we made several statistical and theoretical assumptions that may have shaped our results. These assumptions primarily concern how we quantify plant active periods (for understory wildflower phenology and canopy close phenology) and how we filtered observations, species, and grid cells. For the sake of full transparency, Table S3 (Appendix S1) contains a list of assumptions (including those associated with our statistical analysis in Goal 2) and the justifications for making them.

Goal 2: Spatial patterns of spring ephemerality

Our second goal was to map spatial patterns of number of spring ephemeral species (richness) and the proportion of total species in each cell that are considered spring ephemerals. We therefore took the cell-level species lists with ephemerality definitions from Goal 1 and tallied the number of species that were defined as ephemeral in each cell (note that this is not the EI value, rather it is the binary cell-level classification of ones and zeros). We also calculated the proportion of species in each cell that were considered ephemeral among all understory herbaceous species observed in that cell.

We then used generalized linear models to model the relationships between cell-level ephemeral richness and cell-level proportion of species defined as ephemeral and latitude. For the model of ephemeral species richness, we used a Poisson regression. For our model of proportion of ephemeral species (i.e., number of ephemeral species per cell divided by the number of total species assessed per cell), we used a binomial regression. Both models evaluated quadratic relationships between latitude and the responding variable because preliminary analysis indicated that quadratic fits performed better than linear ones. The latitude values used in both models were the central latitudes of each cell. We calculated pseudo-R^2 values for each relationship based on McFadden's R^2 value. Regression analyses were conducted in R (version 4.3.0) using the glm command in the base stats package.

RESULTS

Species-level ephemerality

The 128 (100 × 100 km) grid cells in this analysis contained an average of 82 forest forb species (±57 SD; Figure 1B) among 559 unique understory herbaceous forb species that we evaluated for spring ephemerality. Of these species, 103 (18.4%) had an EI > 0 (Figure 2), indicating that they were ephemeral in at least one of the grid cells in which they occurred. Nineteen of these species (3.4% of total) had an EI = 1, meaning they were ephemeral in every cell in which they occurred (e.g., *Scilla siberica* and *Euphorbia americanum*; Figure 3H, I), while 94 (16.8% of total) had 0 < EI < 1. The remaining 446 species (79.8%) had an EI = 0, meaning that they were never categorized as ephemeral in any cell that they occurred (e.g., *Antennaria virginica* and *Arisaema triphyllum*; Figure 3A, B). Of these, 25 (6.2% of total) were species that were originally classified as having EI > 0 despite being defined as evergreen or semi-evergreen in the primary literature (average EI for these species before adjustment was 0.28 ± 0.26, meaning they had relatively low EI values to begin with). Note that these misclassifications were most likely the result of too few observations of these species in certain cells. For example, iNaturalist observations are known to be biased to heavier spring observation effort (partially as a result of the City Nature Challenge, which typically occurs in May; Di Cecco et al., 2021), leading to the possibility that evergreen species may not be as commonly measured outside of the early growing season. Other research on herbarium collections found that botanists are biased toward collecting plants that are actively flowering (e.g., Panchen et al., 2019). We posit that a similar bias could be present in iNaturalist data where evergreen angiosperms are primarily observed during their flowering period despite being present in the forest year-round. Only six species (*Cardamine angustata*, *Krigia dandelion*, *Muscari botryoides*, *Narcissus pseudonarcissus*, *Scilla siberica* [Figure 3I], and *Viola bicolor*) had an EI = 1 and were observed in more than two different cells, three of which (*Muscari botryoides*, *Narcissus pseudonarcissus*, and *Scilla siberica*) are introduced geophytes that are commonly cultivated.

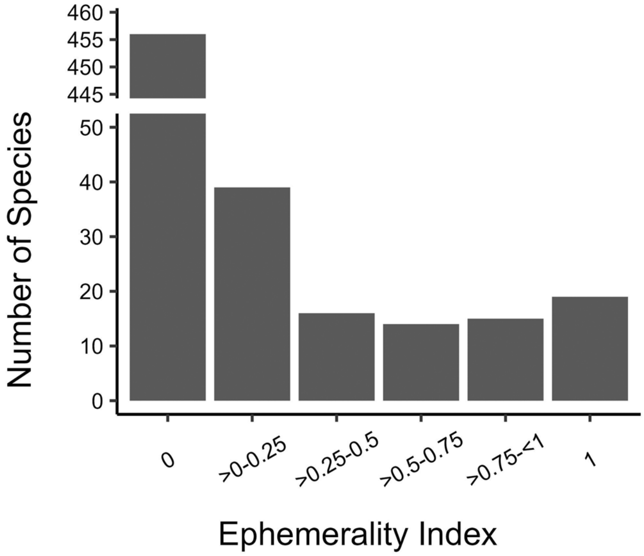

FIGURE 2 Distribution of ephemerality index (EI) values calculated among the 559 herbaceous understory plants in this study. EI values range from 0 (never ephemeral in any grid cell) to 1 (always ephemeral in every grid cell in which it occurs). There is a break in the *y*-axis to better show the variation in the columns with EI > 0.

Of the 94 species with EI values between 0 and 1, 30 of them had EI ≥ 0.5, thereby suggesting a high prevalence of spring ephemerality. For example, *Cardamine americanum* was defined as ephemeral in 55 of the 56 cells it was observed in (EI = 0.98; Figure 3G). Furthermore, despite there being 94 species defined as ephemeral in only part of their range (see Appendices S2 and S3), there was substantial variation in the geographic distribution of cells where species were defined as ephemeral. Some species, such as *Dicentra cucullaria* (EI = 0.54), had no immediately discernible pattern to the distribution of ephemerality across their observed range of cells, with ephemeral and non-ephemeral cells occurring in all parts of their ranges (Figure 3D). Others showed distributions that appeared more directional. For example, *Ranunculus abortivus* (EI = 0.55, Figure 3E) was primarily classified as ephemeral in the southern portion of its range, but not the north. Another example, *Oxalis violacea* (EI = 0.30, Figure 3F), was primarily classified as ephemeral in the western portion of its range and as non-ephemeral in the east. Importantly, 75 of the total 559 species (13.4%) only occurred in a single cell within our data set, with 64 having EI = 0 (e.g., *Antennaria virginica*; Figure 3A) and 11 having EI = 1 (e.g., *Euphorbia mericanum*, Figure 3H). These species may be rare, have highly constrained ranges, or potentially be less likely to be observed by amateur observers. Ephemerality index values for these species may thus be somewhat misleading given that they represent a binary value (ephemeral or not), rather than the continuous metric present in species with wide distributions.

Spatial patterns of spring ephemerality

The species richness of spring ephemeral wildflowers across the landscape was strongly associated with latitude. Ephemeral-species richness (Figure 4A, B), total species richness (Figure 4C, D), and the proportion of ephemeral species (Figure 4E, F) all peaked at middle latitudes (approximately 40°N). Importantly, however, the number of all forb species was positively and significantly associated with richness of ephemeral forb species, indicating that grid cells with more species are more likely to have a greater number of spring ephemerals. Still, the statistically significant relationship between latitude and the proportion of species classified as ephemeral in each cell (Figure 4E) suggests that ephemeral species may still be relatively more common at central latitudes irrespective of total understory forb richness.

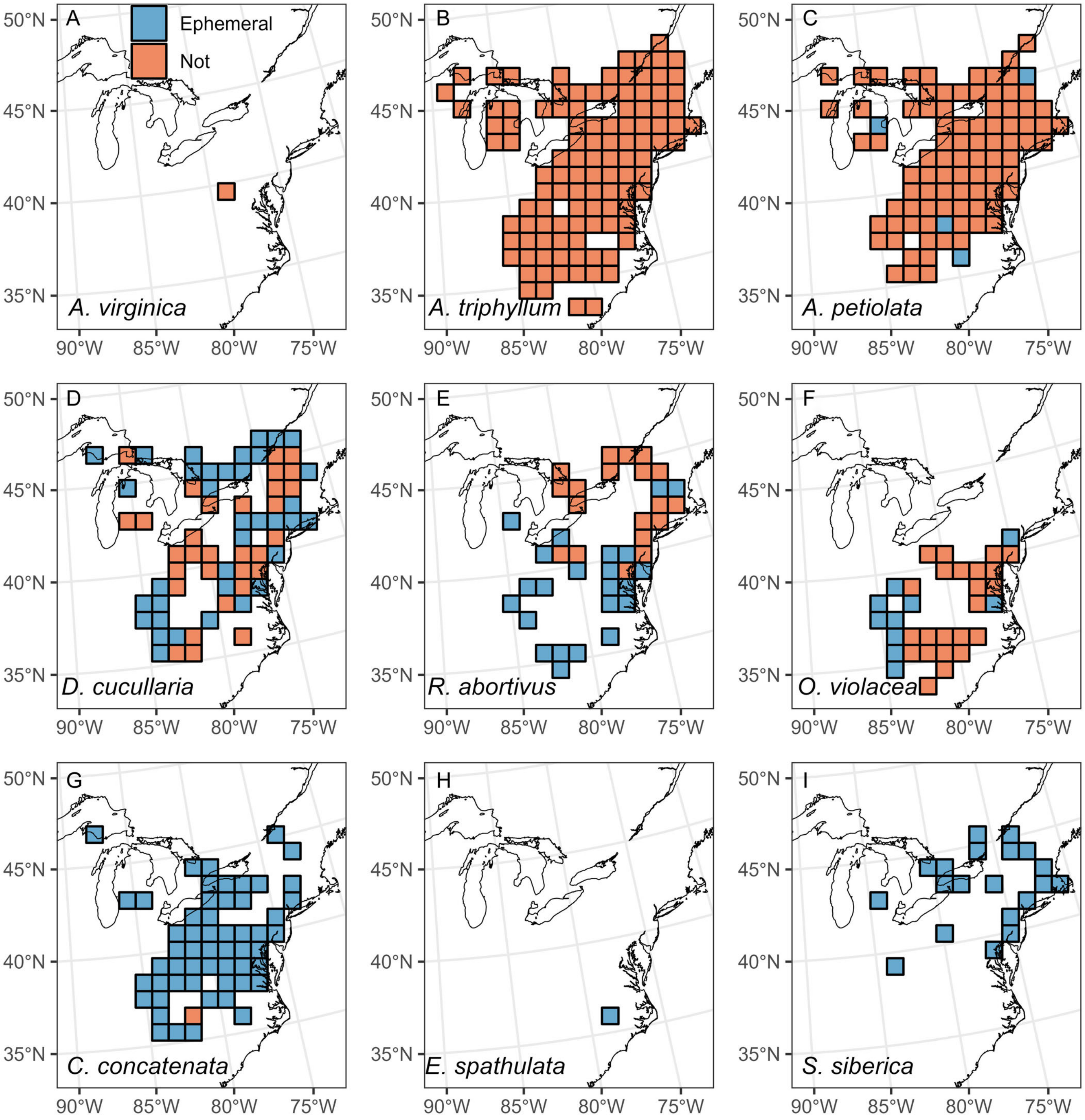

FIGURE 3 Maps showing examples of ephemerality classification for nine species of understory wildflower: (A) *Antennaria virginica*, (B) *Arisaema triphyllum*, (C) *Alliaria petiolata*, (D) *Dicentra cucullaria*, (E) *Ranunculus abortivus*, (F) *Oxalis violacea*, (G) *Cardamine concatenata*, (H) *Euphorbia spathulata*, and (I) *Scilla siberica*. In each panel, 100 × 100 km grid cells are shaded blue if the species was defined as ephemeral or shaded red if it was not. Absent grid cells indicate that data for that species were not available in that location. Maps of all species with EI > 0 are provided in Appendix S3.

DISCUSSION

Spring ephemerality is a common strategy but varies across space

A large proportion of understory vascular herbaceous species (18.4%) in North American forests met our strict definition of "spring ephemeral" (completing their fruiting, flowering, and senescence before the canopy closure each spring) in at least part of their range. This estimate is four times higher than estimated by Spicer et al. (2020), who defined "true ephemerals" as plants that bloomed between March and May and senesced before 1 July based on descriptions in online flora databases and, importantly, not

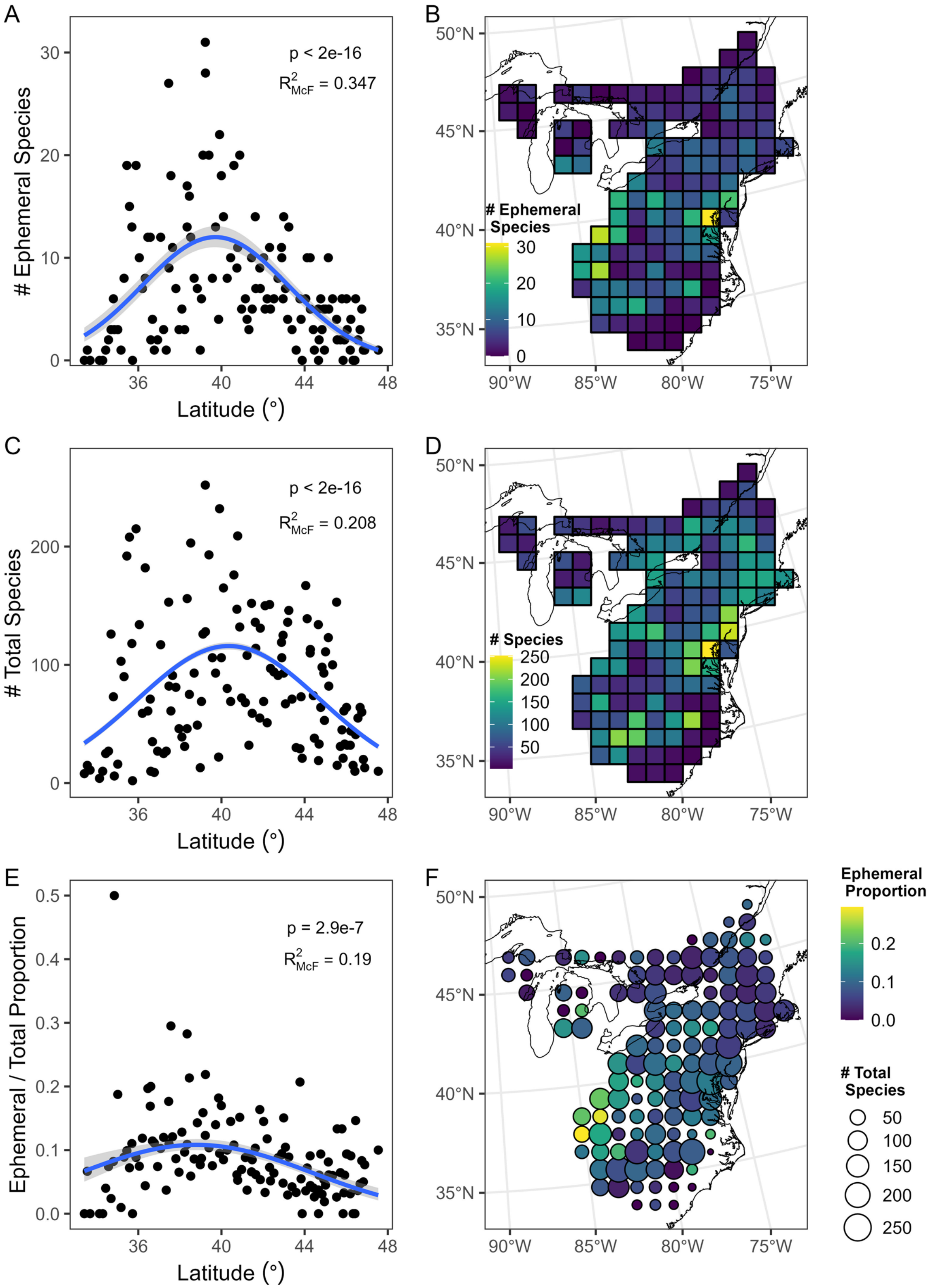

FIGURE 4 Left panels show quadratic relationships between latitude and (A) number (#) of spring ephemeral species, (C) total number of understory forb species, and (E) proportion of total forb species that are spring ephemeral species. Panels (B) and (D) show maps of grid cells with fill color indicating (B) number of ephemeral species and (D) total number of forb species. Colored circles in panel (F) are centered on the corresponding grid cells, with circle size indicating total number of forb species and color indicating proportion of total forb species that are defined as spring ephemerals. The cell in panel E with proportion of ephemerality = 0.5 ($N = 4$ species) was omitted from panel F to better represent variation across the rest of the grid. The unaltered version of panel F is provided as Appendix S1 (Figure S5).

accounting for differences across species' ranges. Spring ephemeral wildflower species were found across the entire extent of eastern deciduous forests covered in this study, with spring ephemeral life history strategies identified as far south as Georgia, United States and as far north as Quebec and Ontario, Canada.

Importantly, only 19 of the 559 understory herbaceous species we assessed (3.4%) were ephemeral in every cell in which they were observed (i.e., EI = 1). Further, only six of these species (*Cardamine angustata, Krigia dandelion*, *Muscari botryoides*, *Narcissus pseudonarcissus*, *Scilla siberica*, and *Viola bicolor*) were observed in more than two cells, suggesting that "true ephemerality", where a species is defined across its entire range, is rare in widely dispersed species. Notably, half of these species (*Muscari*, *Narcussus*, and *Scilla*) are not native to eastern North America. It is thus likely that they evolved this ephemeral strategy under different conditions and are benefitting from their strong ephemerality to become widespread (Fridley, 2012). Still, several wide-ranging species had high EI values very close to one (e.g., *Cardamine mericanum*; Figure 3G), suggesting that a lack of wide-ranging true ephemerals may be partially precluded by exceptional individuals or populations that have anomalously late phenology that is not reflective of a species as a whole.

There are some caveats to this interpretation, however. First, individual plant performance is affected by access to light at the microclimate scale, not at the scale of hundreds of kilometers. As such, our 100 × 100 km estimates of canopy–understory overlap may be too coarse to accurately estimate species-level ephemerality characteristics, especially if access to spring light affects annual survival probability, which has been shown for some understory tree species (Lee and Ibáñez, 2021a). Ephemeral wildflower species may be more likely to be found in forest microenvironments with delayed canopy closure at a resolution much finer than the data we used in this analysis (Dion et al., 2017).

Another important caveat in the interpretation of our results is that both understory and overstory phenology are shifting in response to climate. Several recent studies provided evidence that canopy tree phenology is shifting earlier in the year at a faster rate than understory wildflower phenology is shifting (Heberling et al., 2019b; Tessier, 2019; Lee et al., 2022; Miller et al., 2022; Lorer et al., 2024; but see Alecrim et al., 2022), a pattern that has continued for at least the past 120 years and is projected to continue into the future. Because we estimated wildflower active period length from observations made recently (2015–2021), it is likely that our results reflect higher overlap between wildflower and tree phenology than historically occurred and, therefore, that our results are likely biased in favor of conservative ephemerality estimates. Furthermore, because access to spring light is expected to be reduced even more in the future (Lee et al., 2022), it is possible that historically ephemeral species will no longer meet our strict definition under warmer future spring conditions. The population consequences of this environmental shift could be large (Heberling et al., 2019a). This 7-year-long window also relied on non-standardized surveying from volunteers on the platform iNaturalist and other community science platforms, where the sampling effort is not uniform across species' ranges leading to spatial discrepancies among observations, which limits the representation across ranges (Di Cecco et al., 2021).

The fact that the majority of the information used in this analysis was community science data constitutes an interesting trade-off between data quality and ecological generalizability. On one hand, our results are influenceable by the quality and scope of community-science observations, which can be problematic given that the data we used rely on users that recorded information based on non-uniform (and unrecorded) sampling effort. Thus, even though the majority of community science observations on platforms such as iNaturalist come from a small minority of users that are often classically trained taxonomists (Campbell et al., 2023; White et al., 2023), unequal sampling effort across space and, importantly to this study, throughout the growing season, prevent us from evaluating controls common to biodiversity studies and the effects that sampling effort discrepancies could have on our results. On the other hand, a significant strength of our approach is that the broad geographic scales of the available data allowed us to apply our results across the eastern North American temperate deciduous biome. This point is particularly important because of our finding that the spring ephemerality strategy is not a simple binary, but rather a gradient in plant resource acquisition that is highly variable. Without the geographical range present in this data set, we would have been unable to assess these broad spatial patterns.

Although our continuous ephemerality index likely differs slightly from several traditional classifications of various species, similar information about their phenological strategies is still largely retained. Species like *C. mericanum* are still defined as highly ephemeral from their high EI values, even with EI < 1 indicating it is not a "true" spring ephemeral. Furthermore, the potential bias applies to species with EI values very close to zero as well, such as with *Alliaria mericanu*, a biennial with an overwintering basal rosette (Figure 3C). Such examples imply that potential misclassifications evenly affect species from across the gradient of ephemerality and suggest that our overall conclusions about where ephemerality occurs across the landscape are robust. We argue that this nuanced difference provides researchers and practitioners with a fuller context with which to differentiate among species phenological strategies.

Still, our results indicate that the vast majority of spring ephemeral wildflowers only exhibit ephemeral behavior in a portion of their range, suggesting that inconsistencies in past species-level designations could be the result of range-level differences in expressed phenology. For example, *Trillium grandiflorum* is a charismatic spring-active wildflower with a wide range spanning eastern North America and that is commonly referred to as a spring ephemeral in the scientific literature (e.g., Lubbers and Lechowicz, 1989; Irwin, 2001; but see Lapointe, 2001 for an example of where it is cited as a spring-active wildflower). In contrast, *T. grandiflorum* had an EI value of 0.35, suggesting that this species is likely not a true ephemeral, albeit with ephemeral designations occurring across the species' observed range (see ephemerality maps in Appendix S3). This incongruence could arise from the fact that *flowering* occurs and is generally completed, before the initiation of canopy closure in this species. Individuals maintain their leaves and develop fruit until well into the summer shady period, which indicates a spring-active, but not ephemeral, wildflower species. We suspect that most observers who classify *T. grandiflorum* as a spring ephemeral are likely doing so on the basis of their flowering phenology alone, rather than their activity period as a whole. To resolve this potential confusion, we recommend that such discrepancies should be investigated on a species-by-species basis in the future, with multi-year observations on the same individuals and populations when possible (Lorer et al., 2024).

Range-level variation in ephemerality is further important because it suggests that species are likely to be variably vulnerable to climate change in different parts of their range. Previous work suggests that North American spring ephemerals are likely to lose access to spring light under warming climates as tree leaf out timing increases at a faster rate than wildflower emergence in the spring (Heberling et al., 2019b; Tessier, 2019; Lee et al., 2022; Miller et al., 2022; Lorer et al., 2024; but see Alecrim et al., 2022). Thus, in areas where wildflowers have particularly large windows of spring light (and therefore areas where they are more likely to be defined as ephemeral in this study), they may be less vulnerable to reductions in spring light compared to those in areas where their springtime activity already overlaps with closed-canopy conditions. However, it is difficult to derive strong conclusions from observational studies, such as this one, and the strength of this speculation needs to be evaluated with field-based experiments.

There was also substantial variation in how intraspecific ephemerality designations were distributed across the landscape, suggesting that different ecological mechanisms may control different species' phenological strategies. For example, species like *Dicentra cucullaria* (Figure 3D) appeared to have a relatively random distribution of cells where it was and was not considered ephemeral. In contrast, other species like *Ranunculus abortivus* and *Oxalis violacea* (Figure 3E, F) had distributions of ephemerality that appeared to respectively correlate with either latitudinal or longitudinal gradients. In the case of *R. abortivus*, cells where it was classified as ephemeral were clustered primarily in the south, while cells where it was not classified as ephemeral were clustered primarily in the north. Maps of the ephemerality distributions of all 103 species with EI > 0 are included in Appendix S3.

Latitudinal patterns of spring ephemerality

Results from our models indicate that ephemeral species are most common in central latitudes, with peak ephemeral richness at around 40°N (Figure 4A). Peak proportion of ephemeral species relative to total forb biodiversity occurred slightly more south at around 38°N (Figure 5C). This strong association with latitude could reflect a trade-off between frost and shade avoidance strategies. Spring ephemeral activity is bounded at the beginning of their growing season by the risk of damage from frost events (Augspurger and Salk, 2017). If these species emerge from dormancy too early, late-season frosts can damage foliar and floral tissue (Gezon et al., 2016; Augspurger and Salk, 2017), thereby limiting carbon gain and reproductive success. In worst-case scenarios, frost damage can cause whole-plant mortality. Emerging too late in the growing season, while minimizing risk of frost damage, can instead limit understory plants' access to elevated light availability before canopy closure, thereby limiting their photosynthetic activity. This balance between frost avoidance and shade avoidance, a strategy often referred to as phenological escape (Jacques et al., 2015; Heberling et al., 2019a, Lee and Ibáñez, 2021a, b; Lee et al., 2024b), directly determines a spring ephemeral's capacity for annual carbon assimilation (Heberling et al., 2019a). The duration of phenological escape then cascades to affect seed set success, growth, and survival of spring-active and ephemeral wildflower species (Kudo et al., 2008); access to early seasonal light is therefore a strong selective pressure that determines how and where these species can persist across the landscape.

Temperate forests at both the northern and southern extremes of eastern North America may potentially have a higher composition of evergreen tree canopy species, as the forest type transitions to northern hardwoods–pine/hemlock and oak–pine or subtropical evergreen, respectively (Dyer, 2006), or overall extremes in deciduous canopy phenology. At these range limits, there is thus less room for opportunistic light exposure for understory wildflowers early in the growing season. Furthermore, in northern regions, it is also likely that the window of favorable growth conditions before canopy closure is not beneficial for species utilizing the spring ephemeral strategy because of frost limitations. That is, the duration between the date of last frost and canopy closure decreases with latitude, resulting in a duration of light availability too short to support the spring-ephemeral life history strategy (Neufeld and Young, 2014). In southern latitudes, the window for optimal growth likely extends much longer, where species can take advantage of windows of high light in both the early spring and in late fall, after canopy leaf fall, making the evergreen strategy more advantageous than a purely ephemeral strategy in southern deciduous forests (Neufeld and Young, 2014). This notion is supported by previous research in eastern North America, which found that dominant forest canopy type influenced understory species richness, with highest richness observed in northern hardwood forests and relatively lower richness in evergreen and mixed-deciduous forest types (Ellum et al., 2010), echoing the results we found with respect to understory species richness in this study (Figure 4D). For these reasons, we speculate that forest overstory composition and phenology plays a strong limiting role in the distribution of ephemerality across the landscape.

Microenvironmental conditions also likely play strong roles in determining where ephemeral wildflower species occur across eastern North America. Environmental drivers such as spring temperature, spring precipitation, and winter snowpack, as well as geographic drivers such as elevation, all likely play important roles in modifying phenological strategies within species and large-scale patterns of spring ephemerality among understory communities (De Frenne et al., 2021). We were unable to address the potential influence of these drivers in this study because of the relatively coarse scale (100 × 100 km grid cells) that we used to evaluate latitudinal relationships. For example, previous research found that microenvironmental variation in spring temperature forcing differently affects wildflower phenology at the scale of tens to hundreds of meters (McDonough MacKenzie et al., 2019; Tessier, 2019; Lorer et al., 2024), meaning that evaluating these relationships at coarser resolutions would be difficult and potentially misleading. Similarly, environmental conditions covary strongly with elevation at the scale of tens to hundreds of meters, especially along the Appalachian Mountains at the center of our study region. Gaining a full understanding of how these biogeographic drivers shape spring ephemeral distributions will require analysis with much finer resolution of both phenological observations and environmental conditions where the plants have been observed.

Finally, it is important to note that historical environmental conditions likely played a large role in the current distributions of the wildflowers we addressed here. For example, the last glacial maximum in eastern North America covered the northern portions of these deciduous forests, displacing both over- and understory species (Whitney, 1996; Dyer, 2006). Following the glacial retreat, the migration of these species from refugia was largely limited by the rate and mechanism of dispersal (Cain et al., 1998; Vellend et al., 2003). This glacial boundary and dispersal limitation, and the possibility that the ephemeral strategy is not advantageous in southern forests, could explain the peak in ephemeral richness and proportion around 40°N and 38°N, respectively, because these latitudes are just south of the southernmost ice margin of the last glacial maximum (Whitney, 1996; Dyer, 2006). Additionally, anthropogenic land-use history over the last several centuries introduced novel disturbances to these ecosystems and has led to changes in forest composition and habitat fragmentation across the landscape (Whitney, 1996; Dyer, 2006). The recolonization of understory forb communities in these disturbed forests are again limited by dispersal (Singleton et al., 2001; Bellemare et al., 2002). Due to this, we speculate that ephemeral richness is likely greatest in areas with less human disturbance, such as the central Appalachian region where we found some of the highest species richness of spring ephemeral wildflowers in this study.

CONCLUSIONS

Spring ephemeral wildflowers are ubiquitous in eastern North American temperate forests, but to date this charismatic group has lacked strict definition and biogeographic description. Here, using remote sensing and community science data across species' ranges (Gallinat et al., 2021), we showed that spring ephemeral wildflowers are a diverse group of species that comprise a considerable amount of total understory biodiversity. Further, we found that species' phenological strategies are not fixed across their range, with many species that are often colloquially referred to as ephemeral lacking that trait in parts of their geographic distribution. Lastly, we found preliminary evidence that continental-scale latitudinal gradients are correlated with the distribution of spring ephemeral wildflower species across the landscape. Taken together, these lines of evidence suggest that the geographical distribution of the spring ephemeral phenological strategy is shaped by both current and historical environmental conditions. Although further research is needed to tie patterns of spring ephemerality to microenvironmental variation, recent research suggests that spring ephemeral wildflowers may be particularly vulnerable to the effects of ongoing climate change (Heberling et al., 2019b; Lee et al., 2022). Thus, the definitions of spring ephemerality we provide here will serve as an important ecological baseline with which to establish conservation priorities and to evaluate responses of this biodiverse group to future environmental change.

AUTHOR CONTRIBUTIONS

A.J.Y., B.R.L., and J.M.H. contributed to the conceptual design of the project and wrote the first draft of the manuscript. A.J.Y., B.R.L., J.M.H., and M.E.S. contributed to the data acquisition. B.R.L. was responsible for statistical analyses. All authors contributed to the interpretation of results and analyses and writing and revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Observational data used in this manuscript are permanently archived with GBIF at https://doi.org/10.15468/dd.zyywht. All ephemerality data (and associated metadata) are provided in supplementary data files listed in Appendix S3 and are available for download at https://doi.org/10.5281/zenodo.10015914.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally shareable data necessary to reproduce the reported results. The data are available at https://doi.org/10.5281/zenodo.10015914, https://doi.org/10.15468/dd.zyywht.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplemental figures and tables.

Figure S1. Number of observations from different types of data sources used in this study. A full list of the 72 different data sources is provided in Appendix S2.

Figure S2. Modeled fits of how (A) ephemeral species richness and (B) proportion of ephemeral species relative to total understory herbaceous species richness relate to latitude. Points represent cell-level values of the responding variables with different colors indicating different estimation indices. Indices beginning with "p" are based on ephemerality definitions using the *phenesse* package whereas those beginning with "q" are based on quantile estimates of raw data. The end of the index names reflect either the 95th or 99th percentile cutoff point. Relationships were fit using the default Loess fit in the stat_smooth command of the ggplot2 package, and gray shading represents 95% confidence intervals.

Figure S3. Map of the original 1089 (100 × 100 km) grid cells considered in data set generation. Colors indicate whether cells were included (green, n = 128) or excluded due to one of four criteria (in order of filtering steps): lack of iNaturalist data for species in the combined species list (white, n = 482), being too far away from sites where species lists were assembled (grey, n = 443), too few observations of species in filtered species list (red, n = 5), grid consisted of over 50% water cover by area (blue, n = 17), or estimated day of canopy close was biased by summer-green crop cover (gold, n = 14). Black points show the locations of the 16 sites used to create the combined species list.

Figure S4. Species-level relationships between average canopy close date (day of year) and average species end of season (EOS, day of year). Averages were calculated only using cells where a species was present. Solid black line is the 1:1 line, so points below the line tend to senesce before canopy closure, and those above it tend to maintain activity into the growing season. Point colors indicate species-level ephemerality index (EI) values ranging from never ephemeral (EI = 0, purple points) to always ephemeral (EI = 1, yellow points). The 25 evergreen species for which EI values were manually changed to zero (despite being estimated as being ephemeral in at least part of their range) are indicated with red points.

Figure S5. Full version of Figure 4F in the main text, which omits the cell centered at 34.84695°N, −77.71915°W. This cell had an abnormally large proportion of ephemeral species (0.5) because there were only four species that were assessed in that location.

Table S1. List, source, and location of site species lists used to amass the initial understory plant species list used in this study. Sources are given in the References at the end of Appendix S1.

Table S2. List of evergreen species that were misclassified as spring ephemeral in at least one 100 km × 100 km grid cell and their initial ephemerality index (EI) values. These species were manually assigned EI values of zero in the statistical analysis (see Methods).

Table S3. List of theoretical and statistical assumptions included in this analysis along with their justifications.

Appendix S2. Supplemental data descriptions.

Appendix S3. Ephemerality maps.

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