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Safeguarding the rare woodland species *Gagea spathacea*: Understanding habitat requirements is not sufficient

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Abstract

A large proportion of temperate forest plant diversity is found in the herb layer. However, for many of its species, little is known about their autecology, which makes it difficult to assess potential threats and efficiently safeguard the diversity of understorey herbaceous communities. This also applies to Gagea spathacea (Liliaceae), a globally rare spring geophyte, which mainly occurs in deciduous forests of northern Central Europe. We investigated the causal relationships between population characteristics of G. spathacea and abiotic site conditions across different forest communities in the center of its distributional range. Leaf length (a surrogate of the species' vegetative propagation) was positively related to soil moisture and soil nitrogen. Consequently, mean leaf length was highest in moist forest communities of the alliance Alno-Ulmion. Moreover, mean variability in leaf length was lowest in those forests, indicating a higher and more stable vegetative propagation via bulbils. We found no support for a significant relationship between leaf length and leaf density or between leaf length and flower formation. Population density varied strongly among forest sites, but was not related to soil moisture and hardly influenced

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by soil nitrogen. Our results suggest that soil water and nutrient supply play a vital role in determining the species' vegetative propagation, whereas the duration of habitat continuity is most likely an important determinant of population size and density. Conservation strategies therefore require a better understanding of the complex interrelationships between abiotic site conditions and the historical context-dependency of habitats.

KEYWORDS

ash dieback, biodiversity, dispersal, habitat continuity, herbaceous layer

1 | INTRODUCTION

Habitat loss and habitat degradation are some of the main drivers of global decline in biodiversity (Maxwell, Fuller, Brooks, & Watson, 2016), and subsequent changes in species communities are expected to critically alter the functioning of ecosystems, thus diminishing the benefits that people obtain from nature (Cardinale et al., 2012; Isbell et al., 2017). Biodiversity conservation is therefore becoming a vital societal task in the context of global environmental change (Griggs et al., 2013). To address these challenges, National Biodiversity Strategies and Action Plans have been implemented within the framework of the Convention on Biological Diversity (Chandra & Idrisova, 2011). These national strategies also include lists of species for which individual countries have a particular responsibility (Schnittler & Günther, 1999), based on their global distribution and local abundance. However, our understanding of the habitat requirements of many of these species remains limited, thus limiting the development of effective conservation measures for remaining populations, particularly in the context of global environmental changes.

In temperate forests, the herb layer hosts a large proportion of plant diversity (Gilliam, 2007), and Gagea spathacea (Hayne) Salisb. is one of those temperate woodland plant species for which Germany has a national and international conservation responsibility (Ludwig, May, & Otto, 2007). More than 75% of the species' contiguous world range lies within northern Central Europe (Schnittler, Pfeiffer, Harter, & Hamann, 2009), with the largest populations occurring in the lowlands of northern Germany (Diekmann, Härdtle, & Stoltenberg, 2014; Timukhin, Tuniyev, & Levichev, 2010). The species has been categorized as "vulnerable" in Central Europe (Schnittler & Günther, 1999) and Germany (Metzing, Hofbauer, Ludwig, & Matzke-Hajek, 2018). Moreover, G. spathacea has been assigned the "National responsibility category II," meaning that Germany is responsible for the species to a very high degree, and an extinction in this core area would have very serious consequences for its global population (Gruttke, 2004).

G. spathacea shows hardly any genetic variation, is virtually sterile (Pfeiffer, Klahr, Heinrich, & Schnittler, 2011) and propagates only vegetatively by daughter bulbs ("bulbils;" Pfeiffer, Klahr, Peterson, Levichev, & Schnittler, 2012; Schnittler et al., 2009). The development of bulbils, however, is strongly related to the size of the parent bulb, which in turn is determined by the size of the leaves (Schnittler et al., 2009). Consequently, leaf length can be used as a surrogate for the species' vegetative propagation and dispersal capacity. The fact that the species is confined to ancient forests (Schmidt et al., 2014; Wulf, 1997), i.e., to forests that have been continuously wooded for several hundred years, is largely the result of its extremely low dispersal capacity (dispersal rates of <0.25 cm year⁻¹; Arnold & Fichtner, 2018; Brunet & von Oheimb, 1998). Moreover, G. spathacea is a highly stenoecious woodland species (Diekmann et al., 2014) that is confined to eutrophic and mesotrophic forest communities of the alliances Alno-Ulmion, Carpinion and Fagion (sensu Leuschner & Ellenberg, 2017). However, environmental change-induced shifts in canopy tree species composition might critically alter abiotic site conditions in these forests (Maes et al., 2019). This is particularly relevant for common ash (Fraxinus excelsior), as this species is currently threatened in many parts of Europe (Coker et al., 2019; Needham et al., 2016) and is one of the most abundant tree species in forests hosting G. spathacea populations (Diekmann et al., 2014; Härdtle, 1995). Previous studies provided knowledge on the species' genetics (Pfeiffer et al., 2011, 2012; Schnittler et al., 2009; Westergård, 1936), but how changes in habitat conditions influence the performance and fitness of G. spathacea has remained unclear.

This study aimed to provide a better understanding of the autecology of *G. spathacea*, and thus to identify potential threats to this rare woodland species. We first tested whether the species' performance depends on forest type (Alno-Ulmion, Carpinion and Fagion). We further explored multiple relationships between abiotic site conditions and plant performance measures of *G. spathacea* by using path models. Specifically, we hypothesized (a) that increasing water and nutrient supply promotes leaf length, and (b) that abiotic site conditions (water, nutrient and light availability) influence leaf length indirectly by altering leaf density and flower formation.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

The study was conducted in temperate deciduous forests of northern Germany (Schleswig-Holstein, Mecklenburg-Western Pomerania and Lower Saxony) located within the core distribution area of G. spathacea. Forty populations of G. spathacea were investigated in different forest communities (sensu Leuschner & Ellenberg, 2017): Fagion (Hordelymo-Fagetum and Galio-Fagetum), Carpinion (Stellario-Carpinetum) and Alno-Ulmion (Crepis paludosa-Fraxinus excelsior community and Alno-Fraxinetum). Across forest communities, Anemone nemorosa (90%) and Ficaria verna (86%) were the most frequent spring geophytes. The frequency of other spring geophytes, however, was comparably low: Adoxa moschatellina (10.5%), Gagea lutea (8%), Anemone ranunculoides (3%), Corydalis cava (3%), Allium ursinum (2%) and Arum maculatum (2%). The most frequent summer herbs were Stellaria holostea (71.5%) and Galeobdolon luteum agg. (68%). In each forest, we sampled one to three populations (Figure S1). The sampling of several populations by forest occurred when a forest comprised different community types. Within each population five plots (0.5 m \times 0.5 m) were randomly selected and the corners of the plots were marked with iron bars. To characterize the "optimum" habitat conditions within a population, one plot was located within the area of maximum abundance of G. spathacea (based on visual estimates) and the remaining plots were located in areas that capture (potential) small-scale heterogeneity in habitat conditions within a population. This allowed us to explore how changes in habitat conditions (both within and between populations) affect the performance of G. spathacea.

All populations (except for one: afforestation c. 1800) occurred at ancient forest sites with a continuity of forest cover for at least 250 years, as indicated by the historical maps of Schleswig-Holstein (Vahrendorfsche Landesaufnahme, 1789–1796), Mecklenburg-Western Pomerania (Schmettausches Kartenwerk, 1767–1787) and Lower Saxony (Kurhannoversche Landesaufnahme, 1764–1786). Stand age varied from 95 to 180 years. The predominant soil types were (stagnic) Luvisols, stagnic Gleysols and (humic) Gleysols. The predominant humus type was mull. Soils originated from geological substrates of the Weichselian or Saale glaciation.

In 2015 and 2016, the performance of G. spathacea was recorded from mid-March to the beginning of April in each plot using the number of leaves as a measure of plant density. Moreover, we determined leaf length and the proportion of plants flowering. Average leaf length per plot was quantified as the mean leaf length of at least 30 individuals. To avoid sampling bias, each plot was further divided into 25 subplots $(0.1 \text{ m} \times 0.1 \text{ m})$ and for all individuals within a central subplot leaf length was measured from the aboveground base of the leaf to the terminal leaf tip with a ruler. Note that the number of recorded subplots depended on the abundance of leaves, resulting in 30 to 57 (maximum) measurements per plot. Variability of leaf length was calculated as the coefficient of variation (CV), which is the ratio of the standard deviation of all leaf measurements to the mean leaf length within each plot. We also counted the number of flowering plants (with open or closed flowers) within each plot. Because of the extremely low proportion of plants flowering, which is typical for G. spathacea (Diekmann et al., 2014; Schnittler et al., 2009), we did not analyze the number of flowering plants per plot, but instead the probability that at least one plant per plot produced a flower.

2.3 | Measurements of abiotic habitat conditions

In each plot, soil samples were collected from the upper 5 cm of the mineral soil layer (i.e., within the growing zone of the bulbs) at the four corners of the plot. For subsequent analyses the four subsamples were thoroughly mixed to obtain one composite sample per plot. The samples were analyzed for total carbon (C) and nitrogen (N) concentrations, C/N ratio, exchangeable base cation concentration (EBC), base saturation (BS), cation exchange capacity (CEC) and pH value (measured in a 1:5 soil:water suspension). Total C and N concentrations were determined with a gas chromatographic analyzer (Vario EL, Elementar, Hanau, Germany). Determination of BS, CEC and pH followed standard procedures (Steubing & Fangmeier, 1992).

Local soil water availability was characterized by the mean Ellenberg indicator value for soil moisture (EIV-m) based on the composition of the vegetation that was sampled in 5×5 -m survey plots placed around each plot (note that there was no overlap between vegetation survey plots within a given population). In each vegetation survey plot, we recorded the cover (%) of all vascular plant species (<1.5 m in height) and of all terricolous

bryophytes by visual estimates. Vegetation surveys were conducted in 2015 or 2016 (March/April and June), depending on the sampling date of a specific forest. Each species was assigned an EIV according to Ellenberg et al. (2001) and for each plot we calculated the mean EIV for soil moisture, weighting by species' cover. Mean EIVs characterize the realized ecological niche of a given species along environmental gradients and are commonly applied as surrogates for environmental conditions in vegetation ecology in the absence of directly measured environmental variables (Diekmann, 2003; Schaffers & Sýkora, 2000).

Local light availability at the forest floor during the growing season of *G. spathacea* was quantified by taking hemispherical canopy photos at 1 m above the center of the plot with a digital camera (Nikon Coolpix 4500, Nikon, Tokyo, Japan) with a fisheye lens (Nikon FC-E8 0.21tx). The images were analyzed using the software Optimas 6.5 (Schwalbe, Maas, Kenter, & Wagner, 2009; Wagner, 1998). The program estimates the proportion of total solar radiation penetrating the canopy.

2.4 | Data analysis

We used linear mixed-effects and generalized mixed-effects models to assess the effect of forest type on leaf length (logtransformed), leaf variability, leaf density and flower formation of G. spathacea. Forest (to account for differences in the spatial dependency of populations within the same forest and with the same sampling date) and population (to account for differences in the spatial dependency of plots within the same population) were used as nested random effects. Leaf length and leaf density were modeled assuming a Gaussian error distribution, whereas a binomial error distribution with a logit link was used to model the probability of flowering. Differences in plant performance measures (leaf length, variability in leaf length, leaf density and probability of flower formation) among forest types were further evaluated by a Tukey test. Model validation was assessed and confirmed according to Zuur, Ieno, Walker, Saveliev, and Smith (2009).

We used path analysis (Grace, 2006) based on linear mixed-effects and generalized mixed-effects models to explore possible causal relationships between plant performance (endogenous variables) and abiotic site conditions (exogenous variables). This approach allowed us to explore more mechanistically how linkages between different aspects of plant performance were directly and indirectly affected by changes in the local water, nutrient and light regime. Moreover, we tested if an increase in leaf density or flower formation would result in a reduction of leaf length due to increased intraspecific competition for abiotic resources or increased allocation of resources to flowers. To avoid collinearity between predictors of abiotic site conditions (C, N, C/N-ratio, EBC, BS, CEC and pH value), we selected those covariates that showed no critical correlation according to the variance inflation factor (VIF; Zuur et al., 2009). All VIFs of the selected predictors (N, C/N-ratio, EBC, EIV-m and light) were <1.7. We evaluated different candidate models, each including different combinations of abiotic drivers (N, C/N-ratio, EBC, EIV-m and light). We sequentially dropped non-informative pathways, if their removal resulted in a reduction of the Akaike information criterion (AIC; Grace, 2006; Kline, 2016). The path model was fitted using a piecewise approach allowing for the simultaneous implementation of non-normal distributions and random effects (using the same error structure and error distribution as in the mixed-effects models described above) by combining multiple separate models into a single network using local estimation (Lefcheck, 2016). Path coefficients were standardized to compare their relative importance in the models. Leaf density and soil N concentration were log-transformed prior to analysis to meet model assumptions. Model fit was evaluated based on Fisher's Cstatistics with associated *p*-value (p > 0.05 indicates that sample and observed covariance matrices are not statistically different and thus an adequate fit to the data) (Lefcheck, 2016). All analyses were conducted in R (v3.5.1; http://www.R-project.org) with the packages "lme4" (Bates, Maechler, Bolker, & Walker, 2015), "multcomp" (Hothorn, Bretz, & Westfall, 2008) and "piecewiseSEM" (Lefcheck, 2016).

3 | RESULTS

Across forest types, mean leaf length was 9.3 cm (standard deviation [*SD*], 2.7 cm), mean leaf density (per 0.25 m^2) was 338.5 (*SD*, 239.7) and mean number of flowering plants (per 0.25 m^2) was 1.5 (*SD*, 3.3).

Leaf length and leaf density increased in the order (FA)—Carpinion (CA)—Alno-Ulmion (AU; Fagion Figure 1). On average, leaf length was 29% higher in AU $(p_{adi.} < 0.001)$ than in FA and 16% $(p_{adi.} = 0.052)$ higher than in CA. In contrast, variability in leaf length was 25% higher in FA ($p_{adj.} < 0.001$) and 13% ($p_{adj.} < 0.058$) higher in CA compared to AU. Mean density of leaves in AU was 75% ($p_{adj.} = 0.019$) higher than in FA and 32% $(p_{adi.} = 0.498)$ higher than in CA. The mean probability of flower formation was nearly three times higher in AU than in FA ($p_{adj.} = 0.010$) and CA ($p_{adj.} = 0.021$). In contrast, FA and CA did not significantly differ in the response variables leaf length ($p_{adj.} = 0.514$), variability in leaf length ($p_{adj.} = 0.214$), leaf density ($p_{adj.} = 0.549$) and probability of flower formation ($p_{adj.} = 0.959$). As



Fagion Carpinion Alno-Ulmion Fagion Carpinion Alno-Ulmion

FIGURE 1 Variation in (a) leaf length and (b) variability of leaf length, (c) leaf density and (d) probability of flower formation of *Gagea* spathacea with forest type (Fagion: Hordelymo-Fagetum and Galio-Fagetum; Carpinion: Stellario-Carpinetum; Alno-Ulmion: Crepis paludosa-Fraxinus excelsior community and Alno-Fraxinetum). Predicted responses obtained from mixed-effects models. Error bars indicate standard errors. Different letters indicate significant differences among forest types ($p \le .05$, Tukey test)

TABLE 1 Habitat characteristics of Gagea spathacea popul	ations
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	Across forest types	Fagion	Carpinion	Alno-Ulmion
Ellenberg indicator value for soil moisture	5.81 (0.04)	5.50 (0.05) ^a	5.43 (0.06) ^a	6.11 (0.05) ^b
Light availability (%)	50.30 (0.67)	47.37 (1.31) ^a	46.26 (1.55) ^a	53.32 (0.78) ^b
Species richness	22.22 (0.47)	18.80 (0.69) ^a	19.37 (0.91) ^a	25.12 (0.67) ^b
Soil chemical properties				
pH (water)	4.83 (0.51)	4.81 (0.09) ^{ab}	4.53 (0.09) ^a	4.93 (0.08) ^b
Carbon concentration (C) (%)	6.48 (0.21)	5.54 (0.33) ^a	5.15 (0.34) ^a	7.45 (0.29) ^b
Nitrogen concentration (N) (%)	0.49 (0.15)	0.40 (0.02) ^a	$0.37 (0.02)^{a}$	$0.57 (0.02)^{b}$
C/N ratio	13.25 (0.10)	13.54 (0.24) ^a	13.89 (0.21) ^a	12.87 (0.11) ^b
Exchangeable base cation concentration (mval 100 cm ⁻³)	9.24 (0.32)	8.52 (0.44) ^a	$6.52 (0.47)^{a}$	10.55 (0.49) ^b
Base saturation (%)	60.15 (1.53)	57.16 (2.30) ^a	53.06 (3.18) ^a	64.22 (2.30) ^b
Cation exchange capacity (mval 100 cm ⁻³)	15.62 (0.36)	15.24 (0.64) ^a	$12.70 (0.68)^{b}$	16.81 (0.49) ^{ab}
n (forests)	29	10	6	18
n (populations)	40	12	7	21
n (plots)	200	60	35	105

Note: Soil chemical properties refer to the upper mineral horizon (0-5 cm). Light intensity refers to the forest floor and species richness refers to the ground layer species (vascular plants and terricolous bryophytes) within a 25-m² plot. Values are means and their standard errors (in brackets). Different letters indicate significant differences among forest types (p < .05, Tukey test).

expected, soil moisture (expressed as EIV-m) and nutrient availability (N, C/N-ratio, EBC and BS), light availability and species richness were significantly (all comparisons $p_{adj.} < 0.05$) higher in AU than in FA and CA (Table 1).

The best-fitting path model included soil moisture, soil N concentration and light availability as habitat characteristics that significantly influenced the performance of G. spathacea (Figure 2). The effects of soil C/N ratio and exchangeable base cation concentration on leaf length, leaf density and probability of flowering were not significant (Table S1). Soil moisture (7%), soil N concentration (2%), light availability (1%) and flower formation (1%) accounted for 11% of the variation in leaf length. Leaf length increased with soil moisture (p = .003) and soil N concentration (p = .033). In contrast, light availability had no statistically significant direct (p = .233) or indirect effect (via promoting flower formation; p = .154) on leaf length. Leaf density was positively associated with soil N concentration (p = .088), but not with soil moisture (p = .513). The influence of soil N concentration on leaf density, however, was small (explained variation, 2%) relative to the effect of population identity, which accounted for 47% of the variation in leaf density. There was no significant relationship



FIGURE 2 The best-fitting path model linking plant performance ("length", leaf length; "density", leaf density; "flowers", probability of flower formation) and local habitat conditions (soil nitrogen concentration, soil moisture and light availability). Black and gray arrows denote significant ($^{\circ}p < .10$, *p < .05, ** p < .01, *** p < .001) and non-significant (p > .10) pathways, respectively. Numbers at arrows are standardized path coefficients indicating the effect size of the relationship and arrow width is proportional to the effect size. Percentage values are explained variances of endogenous variables of fixed and random effects; explained variances of fixed effects alone are in brackets. The model provided a good fit to the data (Fisher C = 3.19, degrees of freedom [df] = 4, p = .53) between leaf length and leaf density (p = .719). Light availability (p = .013) and soil moisture (p = .009) had strong positive effects on flowering, whereas the positive effect of soil N concentration was less influential (p = .039).

4 | DISCUSSION

This study provides insights into the autecology of a rare woodland species by showing that soil water and nitrogen are important determinants regulating the leaf length of *G. spathacea*, and thus its vegetative propagation. Soil water and nitrogen were also identified as key habitat characteristics explaining variation in the species' vitality (i.e., leaf density and flower formation). Variation in leaf density, however, was to a large degree explained by population identity, suggesting that factors other than the recorded abiotic site conditions might have a strong impact on the abundance of *G. spathacea*.

4.1 | The role of abiotic site conditions and habitat legacies in the performance of *Gagea spathacea*

Soil nutrient supply is highly important for bulbous plants with a short vegetation cycle (Weeda, 2006), which lasts for c. 3 months in the case of G. spathacea. The species has a high nitrogen demand and is characterized by an exceptionally efficient resorption of nitrogen from senescing leaves and reallocation to bulbs, leading to a twofold increase of the bulbs' biomass at the end of the growing season (Fichtner et al., 2018). This efficient recycling of nitrogen allows the species to avoid nitrogen losses via litter (Aerts, 1990; Thornton & Millard, 1993), and therefore quickly form leaves and new bulbs during its short active growth phase. This explains why leaf length and leaf density increased with increasing soil N concentration. Surprisingly, the concentration of exchangeable base cations and soil C/N ratio were not directly linked with changes of the species' performance, which is likely to be the result of soil moisture-induced changes in the nutrient regime and availability of the soil. In deciduous forests in northern Germany (particularly in stands on ancient moraines), nutrient supply is often confounded with soil moisture (Härdtle, von Oheimb, Meyer, & Westphal, 2003). Thus, forest sites with moist soils are associated with high base supply and low soil C/N ratios in our study (Table 1; Figure S2). On the one hand, a high base supply supports litter turnover, and therefore the provision of nutrients (Härdtle, von Oheimb, Meyer, & Westphal, 2003). On the other hand, increasing soil moisture favors the abundance of tree

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species such as ash (*F. excelsior*) and alder (*Alnus glutionosa*), both of which are characterized by low leaf litter C/N ratios (the latter one due to symbiotic nitrogen fixation). Our finding of increasing leaf length with increasing soil moisture and nitrogen therefore suggests that the relative importance of soil moisture in determining leaf length is largely the result of an increase in soil fertility (in terms of both nitrogen and base supply) via increasing water supply.

G. spathacea develops more bulbils as leaves grow larger in size (up to a maximum of 54 bulbils per plant; Schnittler et al., 2009). Thus, larger plants should be associated with a higher vegetative propagation and therefore with an improved dispersal capacity. Consequently, leaf length should be positively linked to leaf density. Alternatively, it is conceivable that leaf density has a negative effect on leaf length, as increasing intraspecific competition for resources can result in smaller plants and an increase in size inequality (Silvertown & Charlesworth, 2007). Although leaf length decreased with increasing leaf density in FA (Figure S3), we found no evidence for a significant leaf size-density relationship in CA, AU and across forest types. This shows that an increase in leaf length (due to high water and nutrient supply) is less influential in explaining contemporary leaf density of G. spathacea. However, the high importance of population identity, which explained almost half of the variance in leaf density, suggests that habitat continuity is an important determinant of population density. The dispersal capacity of G. spathacea (a plant exclusively relying on subterraneous bulbils for its dispersal; Pfeiffer et al., 2011) is extremely low, because bulbils are generally dispersed over short distances by ants (Graae, 2000; Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999;), by soil translocation through moles and mice (Arnold & Fichtner, 2018) or by uprooting trees (Pfeiffer et al., 2012). Digging by wild boars (Schnittler et al., 2009) and prehistorical farming practices (Arnold & Fichtner, 2018) are further assumed to promote the dispersal of G. spathacea. Stochastic processes that promote effective long-distance dispersal, however, might play a minor role in explaining the species' abundance and population size. For example, studies on temperate forests in northern Germany found that game is an important vector for the endozoochorous and epizoochorous dispersal of vascular plants that are restricted to open landscapes or for species growing in forests as well as in the open landscape, but not for those strongly associated with forests (Heinken, Schmidt, von Oheimb, Kriebitzsch, & Ellenberg, 2006; Schmidt, Sommer, Kriebitzsch, Ellenberg, & von Oheimb, 2004). Given the extremely low dispersal capacity of G. spathacea, it would take a long time to develop a large and dense population from a

single bulbil or few founder bulbils. This indicates that the temporal extent of habitat continuity, and therefore the population age, is an important factor influencing the size and density of *G. spathacea* populations. Although data on the duration of habitat continuity were not available for each study site, we found that the largest and densest population of *G. spathacea* was at a site with a continuous forest cover of *c.* 2,500 years (Arnold & Fichtner, 2018; Figure S4). Population density might also be regulated by interspecific competition during the vegetation cycle of *G. spathacea*, but leaf density of *G. spathacea* was not significantly affected by the mean cover of other spring geophytes in our study (Figure S5).

We found no support for a trade-off between leaf length and flower formation. Although increasing light availability in combination with an ample water and nutrient supply promoted flowering, a higher probability of flowering does not result in a decline of leaf length (i.e., carbon allocation to leaves; Figure 2) or bulb growth (Schnittler et al., 2013). For example, Schnittler et al. (2009) reported that G. spathacea continues to allocate resources to bulbs during flowering. In this context, however, it should be noted that an increase in light availability due to natural or anthropogenic disturbances can favor the growth of winter-green plants (e.g., Rubus spec., G. luteum), that in turn might suppress G. spathacea. This is especially problematic in the Atlantic climate of Schleswig-Holstein, where more frequent mild winters and soil acidification through nitrogen deposition already promote Rubus fruticosus agg., and where G. spathacea has its largest populations. Moreover, closed tree canopies have been demonstrated to be vital for mitigating warming-induced changes in the composition of understorev herbaceous communities, and thus for safeguarding temperate forest plant diversity in the context of climate change (De Frenne et al., 2015).

4.2 | Implications for conservation management

Our results demonstrate the important role of soil water and nutrients in determining leaf length (as a surrogate of vegetative propagation) of *G. spathacea*. Hence, habitat changes that directly or indirectly impair soil water and nutrient availability could have detrimental impacts on the species' reproductive success. For example, a decrease in the abundance of ash due to ash dieback (Münster Mitchell et al., 2014; Needham et al., 2016) is likely to be associated with a decrease in soil nutrients (Münster Mitchell et al., 2014; Thomas, 2016). This is particularly relevant for moist forests, such ash and alder-ash forests, as we found that the largest and most vital populations of

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G. spathacea are currently located in those forests, and alder-ash forests were identified to be most vulnerable to ash dieback (Erfmeier et al., 2019). The ecological consequences of ash dieback for temperate forest biodiversity and ecosystem functioning, however, remain unclear and require further investigation.

The Central European lowland populations of G. spathacea are confined to deciduous forests on ancient forest sites (Schmidt et al., 2014; Wulf, 1997). Hence, the species' occurrence is generally associated with a high diversity of forest species (e.g., Härdtle, von Oheimb, & Westphal, 2003; Nordén et al., 2014; Stefańska-Krzaczek, Kacki, & Szypuła, 2016). Given that within the core distribution area of G. spathacea ancient deciduous forests are rare, it is of vital importance to avoid the conversion of these remaining forests into coniferous or deciduousconiferous stands (Kriebitzsch et al., 2013). Moreover, results from long-term observations of vegetation in a south Swedish deciduous forest suggest that regular soil disturbance by wild boar has a positive effect on the frequency of G. spathacea via reducing the mean cover of more competitive spring geophytes (e.g., A. nemorosa, A. ranunculoides and F. verna; Amelung, 2019; Brunet, Hedwall, Holmströn, & Wahlgren, 2016). Further studies that focus on the impacts of moderate soil disturbance on the performance of G. spathacea may therefore provide improved insight into effective conservation strategies. Our findings highlight that the maintenance of habitat continuity and favorable abiotic site conditions are among the most important measures to safeguard G. spathacea, a species of special conservation interest. This includes, (a) avoiding drainage, and thus preventing soil acidification, (b) promoting autochthonous deciduous tree species in the canopy to maintain a high availability of nutrients, and (c) maintaining closed tree canopies to reduce interspecific competition by winter-green plants and to ensure favorable forest-floor microclimate conditions.

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