The importance of small natural features in forests—How the overgrowth of forest gaps affects indigenous flower supply and flower-visiting insects and seed sets of six *Campanula* species

Ralf Braun-Reichert¹,² | Sven Rubanschi²,³ | Peter Poschlod²

Abstract

1. The abandonment of historical land-use forms within forests, such as grazing or coppicing, and atmospheric nitrogen deposition, has led to an increasing overgrowth of forest gaps and canopy closure in forest ecosystems of Central Europe. From 1945 to 2015, 81% of the forest gaps greater than 150 m² within the study area transitioned into a closed forest.

2. This study investigated how the overgrowth process affects flower supply, flower visitors, and reproduction of *Campanula* species. Six native *Campanula* species with different light requirements were used as phytometers.

3. The forest gaps in the studied area are a feature of the historical European cultural landscape. We compared large gaps caused by human activities, small gaps caused by habitat conditions, and closed forests. In eight blocked replicates, each with the three habitat categories, we recorded the flower cover and number of indigenous flowering species in the immediate surroundings, and, of six *Campanula* species, flower visitors and seed production.

4. Forest gaps and their size positively affected the number of flowering plant species in the surrounding area, the number of all flower visitor groups, and the number of seeds produced by all six *Campanula* species. Flower cover in the surrounding area was higher in large gaps, but there was no difference between small gaps and closed forests. Among flower visitors, small bees varied the most between the three habitat categories, and flies varied the least. The effect on the number of seeds produced was particularly strong for three light-demanding *Campanula* species.

5. The overgrowth of forest gaps negatively affected flower supply, flower-visiting insects, and seed sets of six *Campanula* species. Forest gaps should be managed to maintain the reproduction of open forest plants and their pollinators.

Keywords

bees, *Campanula*, flies, flower visitors, forest management, gap dynamics, pollination
1 | INTRODUCTION

The pollination process is critical for natural and agricultural systems (Guntern et al., 2014; IPBES, 2016; Klein et al., 2006; Naturkapital Deutschland TEEB, 2018). However, this process is threatened in many parts of the world (Leonhardt et al., 2013; Potts et al., 2010; Sanchez-Bayo & Wyckhuys, 2019). In Central Europe, changes in land use are considered the most important cause of the decline in pollinators (MEA, 2005; Zurbuchen & Müller, 2012). Multiple studies in Central Europe (Carrière et al., 2017; Hopfenmüller et al., 2014; Tscharntke et al., 2005; Zurbuchen et al., 2010) assessed open landscapes with regard to management intensity, landscape composition, and configuration or distances between nesting and foraging sites, as well as changes in agricultural landscapes. However, changes in forest landscapes and the associated impacts on pollinating insects have received less research attention, even though forests cover 35% of the area of Europe (MCPFE, 2020).

As light is a prerequisite for many plants to flower, many forest plants flower in spring before the trees unfold their leaves. Additionally, forest edges and open forests are richer in flowers (Burgess et al., 2006; Killkenny & Galloway, 2008). Among pollinating insects, bees are among the most important groups (La Salle & Gauld, 1993). However, forests are generally considered sparsely populated by bees (Westrich, 2018; Winfree et al., 2007; Zurbuchen & Müller, 2012). Nevertheless, gaps in forests offer good habitats even for xero- and thermophilic bee species due to the abundance of food plants and nesting sites (Fuhrmann, 2007; Kohl & Rutschmann, 2018; Westrich, 2018; Wiesbauer, 2017). As well members of Diptera, in particular, hoverflies, are important flower visitors and pollinators in central Europe (Jauker et al., 2012). According to Szymank, Doczkal, et al. (2011), 70%-80% of all German hoverfly species are concentrated in open areas or at the edge of forests.

Unprecedented human-induced changes in the nitrogen (N) cycle in Western Europe in the last century resulted in enormous N deposition from the atmosphere into forest ecosystems (BMEL, 2018; Sutton et al., 2011). Furthermore, the increased atmospheric CO₂ content promoted optimal use of the available N, thereby increasing tree growth rates over the last 50 years (Clais et al., 2008; Laubhann et al., 2009; Thomas et al., 2010). The analysis of 23 studies investigating the effect of atmospheric N deposition on plant communities in understory forests showed densification of the canopy and a shift toward shade-tolerant plant species (Verheyen et al., 2012). In addition to anthropogenic N deposition, the abandonment of traditional land-use practices has caused a significant improvement in the forest nutrient supply, especially within thin soil layers. Historical land-use practices, such as forest litter removal, forest pasture, intensive coppicing, or dead wood collection, led to nutrient impoverishment and, thus, low tree growth rates. Open forests with gaps resulted (Gatter, 2004; Poschlod, 2017; Rubner, 1967). Today, approximately 73% of European forests’ net annual wood increment is utilized by fellings (MCPFE, 2020). For example, in Germany, forest gaps account for only 2% of the forested area (Hamppke, 2018; Schmalfuß & Aldinger, 2012). In a study of the development of forest gaps in a deciduous forest, our research group (Braun-Reichert & Poschlod, 2018) revealed an 81% decrease in forest gaps of more than 150 m² from 1945 to 2015 in the study area. Specifically, historical meadows or pastures are no longer used, and clear cuttings and many small sites naturally treeless due to drought and nitrate deficiency are now overgrown because of recent N deposition.

Nevertheless, little is known about the consequences of the overgrowth of forest gaps on the reproduction of entomophilous plants. A suitable approach to experimentally assess habitat quality or the effects of landscape changes on pollinators is to use attractive potted food plants as phytometers (Steffan-Dewenter et al., 2002; Woodcock et al., 2014; Zurbuchen et al., 2010). Members of the genus Campanula are attractive to flower visitors and suitable as phytometer plants due to the quantity and volume of pollen grains and the amount of nectar they produce (Müller et al., 2006). Furthermore, the genus Campanula attracts the highest number of oligoleptic bee species in Central Europe (Zurbuchen & Müller, 2012). Additionally, flies, especially hoverflies, frequently visit this genus (Hansen & Totland, 2006; Janzon, 1983).

Therefore, this study asked the following questions:

• Is the flower supply as food resources for pollinating insects poorer in a closed forest than in small and large gaps?
• Is the number of Campanula flower-visiting insects lower in a closed forest than in small and large gaps?
• How does the overgrowth of forest gaps affect the seed set of six Campanula species with different light demands?

2 | METHODS

2.1 | Study area

The study area was “Jochenstein,” the easternmost section of the nature reserve “Donauländeit from Passau to Jochenstein.” The nature reserve is located in the Danube valley in southeast Germany, where it borders Austria. The Danube River cuts into the paragneiss rock within the reserve at a depth of approximately 300 m, and the average slope is 30° (LDBV, 2012).

On the south-facing slopes, there is a mosaic of different forest communities. In 36% of the study area, forests with Fagus sylvatica (Luzulo-Fagetum) grow on mesophilic sites, and in 30%, forests with Carpinus betulus and Quercus petraea (Galio-Carpinetum) grow on dry and warm sites. According to aerial photographs of ADBV (Office for Digitisation, Broadband and Surveying Vilshofen, 2013, unpublished data), forest gaps constituted three per cent of the study area. Openness and gaps of the forests may result from the dry site conditions, exposure to the south in combination with thin layers of soil, scree slopes, and exposed rock outcrops. Identified species include Origanum vulgare, Teucrium scorodonia, and Hylotelephium maximum (Geranio-Trifolieta with a transition to Sedo-Scleranthetea). Historical use, such as cuttings, coppicing, removing forest litter, establishing forest pastures, and harvesting leaf fodder, led to further
depletion of soil nutrients. Between 2013 and 2015, the study area received 17–19 kg of additional nitrogen deposition per hectare and year (Schaap et al., 2018). Based on extensive surveys of the nearby power plant and the BIOKLIM-monitoring project (Bässler et al., 2015; Donaukraftwerk Jochenstein, 2012), the insect fauna of the area is known to be particularly species-rich and thermophilic.

### 2.2 Study design

We defined three habitat categories: large gaps (clearings), small gaps (glades), and closed forest. The forest gaps were classified based on their size, measured using aerial photographs (ADBV, Office for Digitisation, Broadband and Surveying Vilshofen, 2013, unpublished data) and QGIS software (QGIS.org, 2018). Small gaps ranged between 32 m² and 375 m² and large gaps between 1,344 m² and 6,008 m² (Table 1). Large gaps were cleared by humans, they resulted for example from road embankments, recent cuttings, nature conservation management measures, or use as meadows (Table 1). Small gaps represent the character of open forest in the study area caused by habitat conditions, namely exposure to the south in combination with thin soil layers, scree slopes, and exposed rock outcrops. We selected sites containing each of these three habitat categories with a maximum distance apart of 210 m to maintain continuity of environmental factors (He et al., 2012). Each site with these three habitat categories formed a statistical block and was replicated eight times (Figure 1). Five blocks were studied in 2015 (blocks A–E) and three blocks in 2016 (blocks F–H; for dates, see Table 2).

Experimental approaches with potted, attractive food plants have proven to be effective in detecting the effects of and on flower visitors (Steffan-Dewenter et al., 2002; Woodcock et al., 2014; Zurbuchen et al., 2010). Six native *Campanula* species occurred in the study area. To demonstrate their utility as phytometers, the list of plants below provides the light requirements, most important habitats, and habitat category in which the species occurred in the study area. The Ellenberg indicator value of light (L) represents the ecological characteristics of Central European plants in relation to the relative light availability in the field, ranging from one (occurring only in deep shadow) to nine (occurring only in full sunlight) (Ellenberg et al., 1991). The list is arranged according to this indicator value. The most important habitats of the species are specified by BfN (1999). Finally, the occurrence in one of the habitat categories in the study area was described. The immediate surrounding area was defined as a square with a 30 m × 30 m side length centered on the pots containing *Campanula*.

- **C. patula**: L = 8; habitats are fresh meadows and pastures; flowered in the surrounding area in large and small gaps.
- **C. glomerata**: L = 7; habitats are dry and semi-dry grasslands; flowered in the study area in large gaps, but not in the immediate surrounding area.
- **C. rotundifolia**: L = 7; habitats are rock sides, wall and scree vegetation, fresh meadows and pastures, dry and semi-dry grasslands, deciduous and coniferous forests of acid and nutrient-poor soils, heathlands, *Nardus* grasslands, and forests and shrubs of dry and warm locations; flowered in the surrounding area in large and small gaps.
- **C. rapunculoides**: L = 6; habitats are fields, field margins, ruderal vegetation, forests and shrubs of dry and warm locations; flowered in small gaps, but not in the immediate surrounding area, and in surrounding area in large gaps.
- **C. persicifolia**: L = 5; habitats are field margins, forests and shrubs of dry and warm locations; flowered in the surrounding area in large and small gaps and closed forest.
- **C. trachelium**: L = 4; habitats are deciduous and fir forests; flowered in the surrounding area in large and small gaps and closed forest.

We grew these six *Campanula* species from autochthonous seeds in pots in an open greenhouse under standardized field conditions: one plant per pot, same pot size, same soil substrate in the pots, and the same water and light conditions within a given

### Table 1 Description of the eight study sites by area of the three habitats (in meter²) and reasons for the openness of the large gaps

| Shortname block | Extension of open area (m²) | Reason for openness of large gap |
|-----------------|-----------------------------|---------------------------------|
| **Closed forest** | **Small gap** | **Large gap** |
| A               | 0              | 80               | 1,344              | Meadow             |
| B               | 0              | 102              | 1,664              | Clearcutting       |
| C               | 0              | 260              | 2,011              | Clearcutting       |
| D               | 0              | 317              | 1,838              | Road embankment in bend |
| E               | 0              | 269              | 2,352              | Road embankment in bend |
| F               | 0              | 175              | 6,008              | Clearcutting       |
| G               | 0              | 375              | 4,651              | Conservation management measure |
| H               | 0              | 32               | 2,451              | Meadow             |
species. We cultivated the plants from seeds for the year 2015 and new ones for 2016. The pots of one species were placed adjacent to each other beside the groups of pots of the other species. The pots of one species were placed in all three habitat categories of a block when the first flower opened. We returned the pots with one Campanula species to controlled garden conditions after the last flower had faded or at the latest when the seed pods opened. In the garden, the species received light according to their needs. As a result, the pots with the Campanula plants were only exposed to the influence of the different habitat categories during the flowering period.

Six pots of each species per site were considered sufficient to lure flower-visiting insects (Sowig, 1989). All pots were placed adjacent to each other in the center of the study sites. We controlled predation, especially by slugs, with slug pellets.

### 2.3 | Flower supply

Every site block was inspected eight times per year. During these eight inspection passes between May and the beginning of August in 2015 and 2016, we recorded the flower supply in the surrounding area (for specific dates, see Table 2). The surrounding area was defined as a square with a 30 m × 30 m side length centered around the pots with Campanula. To measure flower supply, we recorded the coverage of all indigenous flowers in cm² and the number of flowering plants. We summed up the flower cover in cm² per 900 m².

### 2.4 | Flower visitors

During the eight inspections between May and August of 2015 and 2016, when conditions were dry and temperatures 20–28°C, we counted the individual visits of potential Campanula pollinators in the three habitat categories of the eight site blocks. At each inspection pass, we counted the flower-visiting insects of all flowering Campanula plants for one minute, repeated this four times, and then summed up the values. Diptera, bees with body size greater than one cm (large bees) and bees with body size less than one cm (small bees) occurred in statistically evaluable numbers. Beetles, butterflies, and other flower-visiting insect groups were included with flies, small and large bees in the category “all flower-visiting insects.”

### 2.5 | Pollination success

The pots with the Campanula species were returned to controlled conditions in a garden after the last flower had faded and before the first seed capsule had burst open. The timing of this return also minimized the influence of herbivores (snails). To test the pollination success in the different habitat categories, from the six pots in a plot, we collected ten fruits of each Campanula species and counted the number of seeds per fruit.

The six Campanula species in the study area have been deemed self-incompatible (Gadella, 1964; Stephenson et al., 2000). However, depending on the presence of pollinators, self-compatible and even spontaneous selfing plants of the genus Campanula may exist (Inoue & Amano, 1986; Stephenson et al., 2000). Therefore, we verified the self-incompatibility of our Campanula species. For this purpose, we excluded flower visitors on one flower of each species with nylon stockings. Later, we determined if these capsules contained seeds.

### 2.6 | Statistics

We performed two separate linear mixed-effect models to estimate the habitat effect on the flower resources and the number of flowering species in the surrounding area. We added the eight site blocks as random effects in the models due to the experimental design.

Similarly, we analyzed the habitat effect on the occurrence of the four different flower visitor groups. The first group included all recorded flower visitors, which we then divided into the number of small bees, large bees, and flies. For each visitor group, we used a generalized linear mixed-effect model (family="poisson")
in which the number of visitors was used as response variables and the habitat categories as predictors. To control for the design, we again added the eight site blocks as random effects in the models.

To analyze the pollination success, we employed a generalized linear mixed model (family = “poisson”) for each of the six Campanula species. Here, we used the number of seeds as the response variable and the habitat categories as predictors. Similar to the models described earlier, we added the eight site blocks to control for the design.

We used the closed forest as the intercept because the deviation from the closed forest to the forest gaps is the effect of interest.

### 3 | RESULTS

#### 3.1 | Flower supply

Flower cover in the area surrounding large gaps was significantly greater (estimate, 5,606) than in the closed forest. In contrast, flower cover in the area surrounding closed forest and small gaps did not differ significantly (Table 3). The number of flowering plant species in the surrounding area was significantly greater in the forest gaps than in the closed forest (estimated at 12.28 and 2.25, respectively; Table 3).

When we compare the absolute numbers, we see that the mean flower cover in the large gap was 6,138 cm$^2$ in 900 m$^2$ surrounding area, while it was lower in small gaps (477 cm$^2$) than in closed forest (532 cm$^2$). Especially in the first inspection pass, the flower cover in the forest was very high and changed the ranking of small gaps and closed forest (Figure 2a). The mean number of flowering species of the surrounding area (30 m × 30 m) was 13.4 in large gaps, 3.4 in small gaps, and 1.2 in the closed forest (Figure 2b).

#### 3.2 | Flower visitors

The numbers of all flower visitor groups were significantly more frequent in two-gap habitat categories than in closed forest (Table 4). The deviation between the forest gaps and the closed forest was greatest for the small bees (estimated at 4.1 and 3.7, respectively) and smallest for the flies (estimated at -0.62 and 0.98, respectively). The large gaps were a greater distance from the closed forest than the small gaps at all flower visitors and small and large bees. Only the model for the number of flies showed a greater distance to small (estimate 0.98) than to large gaps (estimate ~0.62; Table 4). All groups of flower visitors showed the lowest abundances in the closed forest (Figure 3). All flower visitors and small and large bees were most frequent in large gaps, while flies were more frequent in small gaps (Figure 3). In the closed forest, the absolute abundances of all visitor groups were less than one individual per count (Figure 3). Flies were in the closed forest most frequent, while bees dominated the forest gaps.
3.3 | Pollination success

The capsules excluded from pollination did not produce any seeds, confirming that spontaneous selfing did not occur. Forest gaps and their size positively influenced the number of seeds in all six studied *Campanula* species (Table 5). All *Campanula* species had the lowest number of seeds in the closed forest. Most species had the highest number of seeds in large gaps, whereas *C. rotundifolia* and *C. rapunculoides* produced more seeds in the small gaps (Figure 4). The deviation of the seed set in forest gaps from that in the closed forest was larger for the light-demanding species *C. patula*, *C. glomerata*, and *C. rotundifolia* (estimated from 2.41 to 5.77) than for the shade-tolerant species *C. rapunculoides*, *C. persicifolia*, and *C. trachelium* (estimated from 0.78 to 1.14; Table 5). Species with an Ellenberg indicator value of light of 7 or 8—*C. rotundifolia*, *C. glomerata*, and *C. patula*—produced a mean of fewer than 10 seeds in the closed forest, while *C. rapunculoides* (L = 6), *C. persicifolia* (L = 5), and *C. trachelium* (L = 4) produced a mean of 41 and 83 seeds, respectively. The highest number of mean seeds was 259 for *C. persicifolia* in large gaps (Figure 4).

4 | DISCUSSION

4.1 | Flower supply

It is well known that light positively affects flower formation even in forest plants (Cao et al., 2017; Cunningham, 1997; Killkenny & Galloway, 2008). This observation is consistent with expectations that the number of flowering species would be higher in small gaps (glades) than in closed forest and highest in large gaps (clearings). However, flower cover was only significantly higher in the large gaps than in the closed forest, but not in the small gaps. We attribute this to the high flower cover of spring geophytes in the "closed deciduous forest" in the first inspection pass in May.

![Table 3](image)

**TABLE 3** The linear mixed-effect models show the effect of habitat category on the flower cover in the surrounding areas and on the number of flowering species in the surrounding areas. We set the closed forest as intercept (ic) throughout to show the deviation (estimate) to the large and the small gap.

| Response                        | Fixed effects | Random effects |
|---------------------------------|---------------|----------------|
|                                 | Estimate  | SE | p       | Group | Variance | SD |
| Flower cover surroundings       |           |    |        |       |          |    |
| Closed forest (ic)              | 532       | 702 | .46    | Block | 945,564  | 972 |
| Small gap                       | −55       | 866 | .95    |       |          |    |
| Large gap                       | 5,606     | 866 | <.001***|       |          |    |
| Number flowering species        |           |    |        |       |          |    |
| Surroundings                    |           |    |        |       |          |    |
| Closed forest (ic)              | 1.16      | 0.84| .19    | Block | 3.24     | 1.80|
| Small gap                       | 2.25      | 0.77| <.01** |       |          |    |
| Large gap                       | 12.28     | 0.77| <.001***|       |          |    |

Abbreviations: p, probability; SD, standard deviation; SE, standard error.

*p < .05; **p < .01; ***p < .001.

**FIGURE 2** (a) Mean flower cover (cm²) of the surrounding areas (30 m × 30 m) of the three habitat categories throughout the eight inspection passes. The dates of inspection passes are in Table 2. (b) The number of flowering plant species (mean and standard deviations) in the surrounding areas (30 m × 30 m) of the two forest gaps was significantly different from that of closed forest in addition to a large standard deviation in all inspection passes (Figure 2a). Thus, when forest gaps are overgrown, flower supply declines.
Flower visitors

If forest gaps become overgrown into closed forests, all the groups of flower visitors studied showed declines in their flower visits. These declines were particularly clear for small bees while hardly noticeable for flies (Table 4). Temperature also varied in each habitat category (shading). We assume that temperature explains the differences in abundances between small bees, large bees, and flies. In warm temperatures, bees are dominant flower visitors, while flies are abundant at more moderate temperatures (Adedoja et al., 2018; Corbet et al., 1993; Herrera, 1997; Hodkinson, 2005; Ssymank, Keams, et al., 2011). However, large bees are not a uniform group with regard to their temperature requirements. Bumblebees may also fly at very cool temperatures. In contrast, certain large bees such as *Megachile* spec. or *Melitta haemorrhoidalis* require warmer temperatures (Westrich, 2018).

Similarly, flower visitors were found to more frequently visit *Campanulastrum americanum* (Killkenny & Galloway, 2008) and *Hosta ventricosa* (Cao et al., 2017) in sunny and open patches than in shaded and forested ones. In contrast, Hansen and Totland (2006) found no difference in the number of flower visitors of *Campanula persicifolia* between forest and meadow habitats in Norway. However, they had counted mainly hoverflies, muscid flies, and few bumblebees. We interpret this as an indication that temperatures in Norway were similarly cool in both forest and meadow, in contrast to the habitats we studied (Adedoja et al., 2018; Ssymank, Keams, et al., 2011).

### 4.2 Flower visitors

If forest gaps become overgrown into closed forests, all the groups of flower visitors studied showed declines in their flower visits. These declines were particularly clear for small bees while hardly noticeable for flies (Table 4). Temperature also varied in each habitat category (shading). We assume that temperature explains the differences in abundances between small bees, large bees, and flies. In warm temperatures, bees are dominant flower visitors, while flies are abundant at more moderate temperatures (Adedoja et al., 2018; Corbet et al., 1993; Herrera, 1997; Hodkinson, 2005; Ssymank, Keams, et al., 2011). However, large bees are not a uniform group with regard to their temperature requirements. Bumblebees may also fly at very cool temperatures. In contrast, certain large bees such as *Megachile* spec. or *Melitta haemorrhoidalis* require warmer temperatures (Westrich, 2018).

Similarly, flower visitors were found to more frequently visit *Campanulastrum americanum* (Killkenny & Galloway, 2008) and *Hosta ventricosa* (Cao et al., 2017) in sunny and open patches than in shaded and forested ones. In contrast, Hansen and Totland (2006) found no difference in the number of flower visitors of *Campanula persicifolia* between forest and meadow habitats in Norway. However, they had counted mainly hoverflies, muscid flies, and few bumblebees. We interpret this as an indication that temperatures in Norway were similarly cool in both forest and meadow, in contrast to the habitats we studied (Adedoja et al., 2018; Ssymank, Keams, et al., 2011).

### 4.3 Pollination success

The results clearly showed that the overgrowth of forest gaps into closed forests negatively affected the seed production of all studied *Campanula* species. As expected, the negative influence was
TABLE 5  The generalized linear mixed-effect models shows the effect of habitat category on the number of seeds of the six *Campanula* species. We arranged the species in decreasing order of Ellenberg indicator value of light (Ellenberg et al., 1991).

| Seed response | Fixed effects | Random effects | Group  | Variance | SD |
|---------------|---------------|----------------|--------|----------|----|
|               | Estimate  | SE  | *p*  |        |     |     |
| *C. patula*   | Closed forest (ic) | 2.20  | 0.16  | <.001*** | Block | 0.18  | 0.43 |
|               | Small gap | 2.69  | 0.04  | <.001*** |       |       |     |
|               | Large gap | 3.00  | 0.04  | <.001*** |       |       |     |
| *C. glomerata*| Closed forest (ic) | 1.15  | 0.17  | <.001*** | Block | 0.19  | 0.44 |
|               | Small gap | 2.41  | 0.06  | <.001*** |       |       |     |
|               | Large gap | 2.65  | 0.06  | <.001*** |       |       |     |
| *C. rotundifolia* | Closed forest (ic) | -2.67 | 0.43  | <.001*** | Block | 0.16  | 0.40 |
|               | Small gap | 5.77  | 0.41  | <.001*** |       |       |     |
|               | Large gap | 5.24  | 0.41  | <.001*** |       |       |     |
| *C. rapunculoides* | Closed forest (ic) | 3.69  | 0.1   | <.001*** | Block | 0.05  | 0.23 |
|               | Small gap | 0.87  | 0     | <.001*** |       |       |     |
|               | Large gap | 0.78  | 0     | <.001*** |       |       |     |
| *C. persicifolia* | Closed forest (ic) | 4.34  | 0.13  | <.001*** | Block | 0.14  | 0.37 |
|               | Small gap | 0.91  | 0.15  | <.001*** |       |       |     |
|               | Large gap | 1.14  | 0.01  | <.001*** |       |       |     |
| *C. trachelium* | Closed forest (ic) | 3.56  | 0.44  | <.001*** | Block | 1.53  | 1.24 |
|               | Small gap | 0.80  | 0.02  | <.001*** |       |       |     |
|               | Large gap | 0.89  | 0.01  | <.001*** |       |       |     |

Abbreviations: *p*, probability; SD, standard deviation; SE, standard error.
*p < .05; **p < .01; ***p < .001.

FIGURE 4  The number of seeds produced in 10 capsules (mean and standard deviation) of the six *Campanula* species in the three habitat categories. We arranged the *Campanula* species in decreasing order of their Ellenberg indicator value of light (Ellenberg et al., 1991). In all species, the number of seeds in small and large gaps differed significantly from that of closed forest.
stronger in light-demanding species, such as \textit{C. patula}, \textit{C. glomerata}, and \textit{C. rotundifolia}, than in less light-demanding species, such as \textit{C. persicifolia}, \textit{C. trachelium}, and \textit{C. rapunculoides}. Although \textit{C. patula} has a higher Ellenberg indicator value for light than \textit{C. glomerata} and \textit{C. rotundifolia}, it demonstrates greater plasticity with respect to light and a generally higher seed number. If forest gaps are overgrown into closed forests, the extremely low seed production becomes a limiting factor for reproduction (extinction debt). Moreover, spontaneous selfing resulting in any seed set could not be detected when excluding pollinators, supporting the validity of our results.

Goodell et al. (2010) revealed similar effects for \textit{Lonicera maackii} in edge and interior forest habitats. Killkenny and Galloway (2008) for \textit{Campanulastrum americanum} in the sun and the shade and Cao et al. (2017) for \textit{Hosta ventricosa} in open and closed forest habitats. In contrast, no significant difference was detected in the number of \textit{Campanula persicifolia} seeds between forest and meadow habitats in Norway (Hansen & Totland, 2006). In the Norwegian study, the number of seeds per fruit was strongly pollen-limited in both habitat categories, possibly indicating that flower visitors were crucial for pollination. In contrast, regarding groups of flower visitors, our study showed differences in pollination success, whereas the Norwegian study did not.

### 4.4 Relevance to conservation

In a previous study, we showed that from 1945 to 2015, 81% of forest gaps larger than 150 m² became closed forest areas (Braun-Reichert & Poschlod, 2018). If we place the results of the habitat categories in this temporal context, then the overgrowth of forest gaps has clear negative effects on the flower supply, the number of flower visitors of \textit{Campanula} species, and the number of seeds they produce.

It is reasonable to suppose that the effects regarding \textit{Campanula} flower supply and the number of seeds are transferable to other plant species of light and open canopy forests (Barbier et al., 2008; Hurskainen et al., 2017). They are often listed as fringe species, for example, typical species of the class Trifolio-Geranietaea. Therefore, we can assume that typical plants of open forests are not only declining due to habitat loss but also because of reduced or missing seed sets, which eventually may result in the extinction of local populations. The historical age of forest gaps plays an especially important role in plant species richness (Husakova & Münzbergova, 2014). For pollinators, forest gaps can play an important role as a small natural feature in closed forest, from which flowers in the surrounding forest are also visited (Poschlod & Braun-Reichert, 2017). In addition, an opening of the tree canopy positively affects the number of other arthropod species (Bussler, 2016; Müller et al., 2007). It is known that butterflies, in particular, have a high diversity in open and coppice forests (Fartmann et al., 2013). Furthermore, light forests and forest gaps are important habitats for other animal groups such as birds or bats (Dietz et al., 2016; Gatter, 2004). Hilmers et al. (2018) illustrated the importance of light in the initial stage of forest succession for the diversity of various organism groups. Forest gaps increase habitat diversity, structural complexity, and faunal and floral species diversity (Muscolo et al., 2014). Historically open forests should be preserved as a part of the European cultural landscape and as important habitat for flora and fauna, especially pollinators.

Only a few decades earlier, open forests and forest gaps were much more common in the cultural landscape of Central Europe (Poschlod, 2017). Now, historical forms of forest use have been abandoned, and nitrogen deposition has increased (Hampicke, 2018; Poschlod, 2017; Stuber & Bürgi, 2011; Verheyen et al., 2012). Even naturally formed gaps are growing over faster than they would without the heavy nitrogen inputs. Especially on marginal sites like rocky heads, where only certain tree species could grow very slowly, are now colonized by atypical tree species with very dense canopies like Fagus sylvatica. Therefore, the political demand for a reduction of nitrogen inputs must be continuously asserted (Sutton et al., 2011).

Maintenance is necessary to preserve forest gaps of high ecological value because, without human intervention, they will close (Braun-Reichert & Poschlod, 2018; Bussler, 2016). However, simple thinning through logging often leads to undesirable effects such as strong growth of \textit{Rubus} spp. or other nutrient-indicating plants. A significant reduction of N deposition is necessary for the long term to preserve forest gaps (Sutton et al., 2011; Verheyen et al., 2012). Historical forms of land use in forests such as forest grazing or coppice are complex (in terms of target species, type of grazing animal, and intensity and duration of grazing) and labor-intensive and therefore not easy to implement (Bärnthol, 2003; Liegl & Dolek, 2008; Poschlod, 2017; Rackham, 2003; Rupp & Michiels, 2020; Zahn et al., 2014). However, grazing animals and coppicing would remove nutrients which contributes to the openness of the forest (Bärnthol, 2003; Berendse, 1985; Marrs et al., 2020). The new development of pristine forests is often set as a conservation goal, which is easier to manage but seemingly contradicts forest gap management. Only seemingly, because forest gaps are small natural features that do not occupy large areas in contrast to pristine forests. However, the implementation of both concepts would greatly increase the diversity of an area and its ecological and nature conservation value.

## ACKNOWLEDGMENTS

We thank Volker Debus and the gardeners of the Botanical Garden of the University of Regensburg for cultivating a multitude of \textit{Campanula} plants, Cristian Odar for the help with data entry, Florian Hartig for the support with statistics, and Martin Lüthke for improving the writing in English. We thank the Government of Lower Bavaria for granting access and seed collecting permits and the Land Survey Office in Vilshofen for providing maps.

## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

Ralf Braun-Reichert: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (lead); Supervision (equal);
Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). Peter Poschlod: Conceptualization (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (supporting); Visualization (supporting); Writing – review and editing (supporting). Sven Rubanschi: Formal analysis (equal); Methodology (equal); Software (supporting); Validation (equal); Writing – review and editing (supporting).

DATA AVAILABILITY STATEMENT

The data of flower supply, flower visitors, and number of seeds that support the findings of this study are openly available in Dryad at http://doi.org/10.1002/ece3.7965.

ORCID

Ralf Braun-Reichert https://orcid.org/0000-0002-3257-3212

REFERENCES

Adedoga, O. A., Kehinde, T., & Samways, M. J. (2018). Insect-flower interaction networks vary among endemic pollinator taxa over an elevation gradient. PloS One, 13(11), e0207453. https://doi.org/10.1371/journal.pone.0207453

Barbier, S., Gosselin, F., & Balandier, P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved — A critical review for temperate and boreal forests. Forest Ecology and Management, 254, 1–15. https://doi.org/10.1016/j.foreco.2007.09.038

Bärnthol, R. (2003). Alderwälder und Biodiversität in der Windsheimer Donauwölfe. (3rd ed., pp. 54). Thurner Akademien der Wissenschaften Schweiz. Factsheets und andere Bestäuber. Bedeutung für Landwirtschaft und Biodiversität. Druckerei des Bundesministeriums für Ernährung und Landwirtschaft (Eds.), pp. 54.

Bauernhansel, H. (2016). Eichenwälder und Biodiversität in der Windsheimer Donauwölfe. (3rd ed., pp. 54). Thurner Akademien der Wissenschaften Schweiz. Factsheets und andere Bestäuber. Bedeutung für Landwirtschaft und Biodiversität. Druckerei des Bundesministeriums für Ernährung und Landwirtschaft (Eds.), pp. 54.

Ciais, P., Schelhaas, M. J., Zaehle, S., Piao, S. L., Cescatti, A., Liski, J., Luysaert, S., Le-Marie, G., Schulze, E.-D., Bouriaud, O., Freibauer, A., Valentini, R., & Nabuurs, G. J. (2008). Carbon accumulation in European forests. Nature Geoscience, 1, 625–630. https://doi.org/10.1038/ngeo233

Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., & Smith, K. (1993). Temperature and the pollinating activity of social bees. Ecological Entomology, 18, 17–30. https://doi.org/10.1111/j.1365-2311.1993.tb01075.x

Cunningham, S. A. (1997). The effect of light environment, leaf area, and stored carbohydrates on inﬂorescence production by a rain forest understory palm. Oecologia, 111, 36–44. https://doi.org/10.1007/s004420050205

Dietz, C., Nill, D., & von Helverson, O. (2016). Handbuch der Pflanzenfamilien – Europa und Nordwestafrika. 2nd ed., (416 pp). Kosmos.

Dexter, D. (2003). Donaukraftwerk Jochenstein/Danube power plant Jochenstein (2012). Erläuterungsbericht Planfeststellungsverfahren Energieversorger Riedl. Retrieved from http://www.landkreis-passau.de/internet-links/Energieversorger_Riedl/JES-A001-VHBD3-B40036-00-CFE.pdf

Ellenberg, H., Düll, R., Wirth, V., Werner, W., & Paulißen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa, 2nd ed. Verlag Erich Goltze KG. Scripta Geobotanica.

Fartmann, T., Müller, C., & Poniatowski, D. (2013). Effects of copicing on butterfly communities of woodlands. Biological Conservation, 159, 396–404. https://doi.org/10.1016/j.biocon.2012.11.024

Frazer, G. W., Canham, C. D., & Lertzman, K. P. (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and Gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York. pp. 36.

Fuhrmann, M. (2007). Mitteleuropäische Wälder als Primärlebensraum von Stechmimen (Hymenoptera, Aculeata). Linzer Biologische Beiträge, 39(2), 901917.

Gadella, T. W. J. (1964). Some cytological observations in the genus Campanula. II. Proceedings of the Royal Netherlands Academy of Arts and Sciences, Ser. C. 66:270–283.

Gatter, W. (2004). Deutschlands Wälder und ihre Vogelgesellschaften im Rahmen von Gesellschaftswandel und Umwelteinflüssen. Vogelwelt, 125, 151–176.

Goodell, K., McKinney, A. M., & Lin, C.-H. (2010). Pollen limitation and local habitat-dependent pollinator interactions in the invasive shrub Lonicera maackii in local habitat-dependent pollinator interactions in the invasive shrub Lonicera maackii. International Journal of Plant Sciences, 171(1), 63–72. https://doi.org/10.1086/647921

Guntern, J., Suhner, M., Neumann, P., & Müller, A. (2014). Bienen und andere Bestäuber. Bedeutung für Landwirtschaft und Biodiversität. Akademien der Wissenschaften Schweiz. Factsheets, 9(1), 9.

Hampicke, U. (2018). Kulturlandschaft. Acker, Wiesen, Wälder und ihre Produkte. Ein Lesebuch für Städter (300 pp). Springer.

Hansen, V.-I., & Totland, O. (2006). Pollinator visitation, pollen limitation, and selection on flower size through female function in contrasting habitats within a population of Campanula persicifolia. Canadian Journal of Botany, 84(3), 412–420. https://doi.org/10.1139/b06-012

He, Z., Liu, J., Wu, C., Zheng, S., Hong, W., Su, S., & Wu, C. (2012). Effects of forest gaps on some microclimate variables in Castanopsis kawakamii natural forest. Journal of Mountain Science, 9, 706–714. https://doi.org/10.1007/s11629-012-2304-y

Herrera, C. M. (1997). Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos, 78, 601–611. https://doi.org/10.2307/3545623
Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. *Journal of Applied Ecology, 5*, 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews, 80*, 489–513. https://doi.org/10.1111/s1467-9230.10006767

Hoiß, B. (2020). Schwebfliegen – vergessene Helfer mit faszinierender Ökologie. – ANLienig Natur 42(1): online preview, (10) pp. Laufen; Retrieved from www.anl.bayern.de/publikationen

Hopfenmüller, S., Steffan-Dewenter, I., & Holzschuh, A. (2014). Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS One, 9* (8), e104439. https://doi.org/10.1371/journal.pone.0104439

Hurskainen, S., Jäkäläniemi, A., Ramulab, S., & Tuomib, J. (2017). Tree removal as a management strategy for the lady’s slipper orchid, a flagship species for herb-rich forest conservation. *Forest Ecology and Management, 406*, 12–18. https://doi.org/10.1016/j.foreco.2017.09.056

Husakova, I., & Münzbergova, Z. (2014). Relative Importance of Current and Past Landscape Structure and Local Habitat Conditions for Plant Species Richness in Dry Grassland-Like Forest Openings. *PLoS One, 9*(5), e97110. https://doi.org/10.1371/journal.pone.0097110

Inoue, K., & Amano, M. (1986). Evolution of Campanula punctata Lam. in the Izu Islands: Changes of pollinators and evolution of breeding systems. *Plant Species Biology, 1*, 89–97. https://doi.org/10.1111/j.1442-1984.1986.tb00018.x

IPBES - Intergovernmental science policy Platform on Biodiversity and Ecosystems Services (2016). *Global assessment report on biodiversity and ecosystem services on pollinators, pollination and food production*. Retrieved from www.ipbes.net/global-assessment-rep-ort-biodiversity-ecosystem-services

Janzon, L.-A. (1983). Pollination studies of Campanula persicifolia (Campanulaceae) in Sweden. *Grana*, (Campanulaceae) in Sweden. *Biological Reviews, 100*, 121–148. https://doi.org/10.1016/j. biorev.2010.01.023

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2006). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences, 274*, 303–313. https://doi.org/10.1098/rspb.2006.3721

Kohl, P. L., & Rutschman, B. (2018). The neglected bee trees: European beech forests as a home for feral honey bee colonies. *PeerJ, 6*, e4602. https://doi.org/10.7717/peerj.4602

La Salle, J., & Gauld, I. D. (1993). Hymenoptera; their diversity and their impact on the diversity of other organisms. Hymenoptera. In J. La Salle, & I. D. Gauld (Eds.), *Hymenoptera and Biodiversity* (pp. 1–26). CAB.

Laubhann, D., Sterba, H., Reinds, G. J., & de Vries, W. (2009). The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical tree growth model. *Ecology and Management, 258*, 1751–1761.

LDBV Landesamt für Digitalisierung, Breitband und Vermessung/Agency for Digitisation, High Speed Internet and Surveying (2012). *Geoportal Bayern - Bayern Atlas*. Retrieved from https://geoportal.bayern.de/bayerenatlas/?topic=ba&lang=de&bgLayer=luftbild_labels&catlogNodes=11.1226&ek=848430.968&n=5384910.82&zoom=11&layer=KML%7C%7Chttps%3A%2F%2Fgeoportal.bayern.de%2Fba-backend%2F%2Files%2FF_4b11e2a0-3eb8-11eb-8bc9-a5642ddecde5_bb691179-755a-42ec-a1ad-f6ddf41a14f%7C%7Ctrue

Leonhardt, S. D., Gallai, N., Garibaldi, L. A., Kuhlmann, M., & Klein, A. M. (2013). Economic gain, stability of pollination and bee diversity decrease from southern to northern Europe. *Basic and Applied Ecology, 14*, 461–471. https://doi.org/10.1016/j.baae.2013.06.003

Liegl, A., & Dolek, M. (2008). Conservation of coppice with standards for canopy arthropods: The Bavarian Conservation Programme for Forests. In A. Floren, & J. Schmidl (Eds.), *Canopy Arthropod Research in Europe*. *Basic and applied studies from the high frontier* (pp. 551–562). Bioform.

Marrs, R. H., Lee, H. H. M., Blackbird, S., Connor, L., Girdwood, S. E., O’Connor, M., Smart, S. M., Rose, R. J., O’Reilly, J., & Chiverrell, R. C. (2020). Release from sheep-grazing appears to put some heart back into upland vegetation: A comparison of nutritional properties of plant species in long-term grazing experiments. *Annals of Applied Biology, 177*, 152–162. https://doi.org/10.1111/aab.12591

MCPFE - Ministerial Conference on the Protection of Forests in Europe (2020). State of Europe’s Forests. Bratislava. (8 pp).

MEA - Millennium Ecosystem Assessment (2005). *Ecosystems and human well-being*. Synthesis. Washington. World Resources Institute.

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee-flower relationships. *Biological Conservation, 130*, 604–615. https://doi.org/10.1016/j. bioccon.2006.01.023

Müller, J., Bußler, H., Gößner, M., Gruppe, A., Jarzabek-Müller, A., Preis, M., & Rettelbach, T. (2007). Forest edges in the mixed-montane zone of the Bavarian Forest National Park - hot spots of biodiversity. *Silva Gabreta*, 13(2), 121–148.

Muscolo, A., Bagnato, S., Sidari, M., & Mercurio, R. (2014). A review of the roles of forest canopy gaps. *Journal of Forestry Research, 25*, 725–736. https://doi.org/10.1007/s11676-014-0521-7

Naturkapital Deutschland – TEEB DE (2018). Werte der Natur aufzeigen und in Entscheidungen integrieren – eine Synthese. Helmholtz-Zentrum für Umweltforschung – UFZ, Leipzig. (136 pp).

Poschlod, P. (2017). *Geschichte der Kulturlandschaft*, 2nd ed., Stuttgart. (320 pp).

Poschlod, P., & Braun-Reichert, R. (2017). Small natural features with large ecological roles in ancient agricultural landscapes of Central Europe – history, value, status, and conservation. *Biological Conservation, 211*, 60–68. https://doi.org/10.1016/j.bialcoen.2016.12.016

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution, 26*(4), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

QGIS.org (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from http://qgis.org

Rackham, O. (2003). *Ancient Woodland: its history, vegetation and uses in England*, 2nd ed. Castlepoint Press.

Rubner, H. (1967). *Forstgeschichte im Zeitalter der industriellen Revolution. Schriften zur Wirtschafts- und Sozialgeschichte 8*. Duncker & Humblot.

Rupp, M., & Michiels, H. G. (2020). Waldweide im Waldnaturschutz - wood pasture in forest nature conservation. *Mitteilungen des VFSstandort.wald, 51*, 153–172.

Sanchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation, 232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Schaap, M., Hendriks, C., Kranenburg, R., Kuenen, J., Segers, A., Schlutow, A., Nagel, H.-D., Ritter, A., & Banzhaf, S. (2018). PINETI-3: Modellierung atmosphärischer Stoffeinträge von 2000 bis 2015 zur Bewertung der ökosystem-spezifischen Gefährdung von Biodiversität durch Luftschadstoffe in Deutschland. Umweltbundesamt (Hrsg.). Retrieved from https://gis.uba.de/website/depot1/

Schmauß, N., & Aldinger, E. (2012). Lichte Wälder – warum sind sie uns wichtig? *FVA Einblick, 3*(16), 6–9.
Sowig, P. (1989). Effects of flowering plant’s patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia, 78, 550–558. https://doi.org/10.1007/BF00378747

Ssymank, A., Doczkal, D., Rennwald, K., & Dziock, F. (2011). Rote Liste und Gesamtenliste der Schwebfliegen (Diptera: Syrphidae) Deutschlands. In Bundesamt für Naturschutz (BfN) (Ed.), Rote Liste Gefährdeter Tiere, Pflanzen und Pflanzen Deutschlands. Band 3: WirbelloseTiere (Teil 1) (Vol. 70, pp. 13–83).

Ssymank, A., Kearns, C., Pape, T., & Thompson, F. (2011). Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity, 9, 86–89. https://doi.org/10.1080/14888386.2008.9712892

Steffan-Dewenter, I., Münzenberg, U., Bürger, C. H., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83(5), 1421–1432. https://doi.org/10.1890/0012-9658(2002)083%5B1421:SDEOL C%5D2.0.CO;2

Stephenson, A. G., Good, S. V., & Vogler, D. W. (2000). Interrelationships among inbreeding depression, plasticity in the self-incompatibility system, and the breeding system of Campanula rapunculoides L. (Campanulaceae). Annals of Botany, 85A, 211–219. https://doi.org/10.1006/anbo.1999.1033

Stuber, M., & Bürgi, M. (2011). Hütterbueb und Heitisträhl – Traditionelle Formen der Waldnutzung in der Schweiz 1800 bis 2000. Haupt Verlag.

Sutton, M. A., Howard, C. M., Erisman, J. W., Billen, G., Bleeker, A., Grennfelt, G., van Grinsven, H., & Grizzetti, B. (2011). Nitrogen in Europe. Sources, effects and policy perspectives. Cambridge University Press.

Thomas, R. Q., Canham, C. D., Weathers, K. C., & Goodale, C. L. (2010). Increased tree carbon storage in response to nitrogen deposition in the US. Nature Geoscience, 3, 13–17. https://doi.org/10.1038/ngeo721

Zahn, A., Berkart-Alcher, B., Kraut, M., Zehm, A., & Adelmann, W. (2014). Online-Handbuch: Beweidung im Naturschutz— Bayerische Akademie für Naturschutz und Landschaftspflege (ANL). https://www.anl.bayern.de/fachinformationen/beweidung/handbuch.htm

Sowig, P. (1989). Effects of flowering plant’s patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia, 78, 550–558. https://doi.org/10.1007/BF00378747

Ssymank, A., Doczkal, D., Rennwald, K., & Dziock, F. (2011). Rote Liste und Gesamtenliste der Schwebfliegen (Diptera: Syrphidae) Deutschlands. In Bundesamt für Naturschutz (BfN) (Ed.), Rote Liste Gefährdeter Tiere, Pflanzen und Pflanzen Deutschlands. Band 3: WirbelloseTiere (Teil 1) (Vol. 70, pp. 13–83).

Ssymank, A., Kearns, C., Pape, T., & Thompson, F. (2011). Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity, 9, 86–89. https://doi.org/10.1080/14888386.2008.9712892

Steffan-Dewenter, I., Münzenberg, U., Bürger, C. H., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83(5), 1421–1432. https://doi.org/10.1890/0012-9658(2002)083%5B1421:SDEOL C%5D2.0.CO;2

Stephenson, A. G., Good, S. V., & Vogler, D. W. (2000). Interrelationships among inbreeding depression, plasticity in the self-incompatibility system, and the breeding system of Campanula rapunculoides L. (Campanulaceae). Annals of Botany, 85A, 211–219. https://doi.org/10.1006/anbo.1999.1033

Stuber, M., & Bürgi, M. (2011). Hütterbueb und Heitisträhl – Traditionelle Formen der Waldnutzung in der Schweiz 1800 bis 2000. Haupt Verlag.

Sutton, M. A., Howard, C. M., Erisman, J. W., Billen, G., Bleeker, A., Grennfelt, G., van Grinsven, H., & Grizzetti, B. (2011). Nitrogen in Europe. Sources, effects and policy perspectives. Cambridge University Press.

Thomas, R. Q., Canham, C. D., Weathers, K. C., & Goodale, C. L. (2010). Increased tree carbon storage in response to nitrogen deposition in the US. Nature Geoscience, 3, 13–17. https://doi.org/10.1038/ngeo721

Tschamtke, T., Klein, A. M., Krues, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters, 8, 857–874.

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédi, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., ... Verstraeten, G. (2012). Driving factors behind the eutrophication signal in storend plant communities of deciduous temperate forests. Journal of Ecology, 100, 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Westrich, P. (2018). Die Wildbienen Deutschlands. Eugen Ulmer.

Wiesbauer, H. (2017). Wilde Bienen. Biologie- Lebensraumdynamik am Beispiel Österreich - Artenportraits. Ulmer.

Winfree, R., Grisworld, T., & Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21(1), 213–223. https://doi.org/10.1111/j.1523-1739.2006.00574.x

Woodcock, T. S., Pekkola, L. J., Dawson, C., Gadallah, F. L., & Kevan, P. G. (2014). Development of a Pollination Service Measurement (PSM) method using potted plant phytometry. Environmental Monitoring and Assessment, 186, 5041–5057. https://doi.org/10.1007/s10661-014-3758-x

Zahn, A., Berkart-Alcher, B., Kraut, M., Zehm, A., & Adelmann, W. (2014). Online-Handbuch: Beweidung im Naturschutz— Bayerische Akademie für Naturschutz und Landschaftspflege (ANL). https://www.anl.bayern.de/fachinformationen/beweidung/handbuch.htm

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Long foraging distances impose high costs on offspring production in solitary bees. Journal of Animal Ecology, 79, 674–681. https://doi.org/10.1111/j.1365-2656.2010.01675.x

Zurbuchen, A., & Müller, A. (2012). Wildbienenschutz - von der Wissenschaft zur Praxis (pp. 162). Haupt.

How to cite this article: Braun-Reichert, R., Rubanschi, S., & Poschlod, P. (2021). The importance of small natural features in forests—How the overgrowth of forest gaps affects indigenous flower supply and flower-visiting insects and seed sets of six Campanula species. Ecology and Evolution, 11, 11991–12002. https://doi.org/10.1002/ece3.7965