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# Seasonal Dynamics of Floodplain Forest Understory–Impacts of Degradation, Light Availability and Temperature on Biomass and Species Composition

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**Abstract:** Forest understory significantly contributes to matter cycling in ecosystems, but little is known about its carbon pool. This is especially poorly understood in floodplain forests, one of the most threatened ecosystems worldwide. We studied seasonal dynamics of biomass and species composition of understory vegetation in degraded and non-degraded floodplain forests, to improve our understanding of carbon pools in forest ecosystems. We hypothesized that degraded and non-degraded floodplain forests will differ in patterns of seasonal variability of biomass and species composition. The study was conducted in Poznań (W Poland) in two study plots (each with 10 samples) across 22 dates (March–November 2016). In each date, we collected understory aboveground biomass. We evaluated impact of light availability and soil temperature on biomass and species composition. Our study revealed high dynamics of biomass production. We found maximum biomass crop of understory in degraded floodplain forest on 24 April (930.12 ± 48.70 kg ha$^{-1}$), whereas in non-degraded floodplain forest the maximum occurred on 30 May (768.99 ± 40.65 kg ha$^{-1}$). At the beginning of the growing season, understory biomass was dominated by spring ephemerals and later these species were replaced by others present for the whole season. Additionally, we confirmed the positive impacts of light availability and temperature on understory primary production. The pattern revealed drove species composition shifts and low differences in biomass crop between consecutive dates. Patterns of understory biomass dynamics differed between degraded and non-degraded plots. Despite study limitations, we provided rare data about understory biomass dynamics of floodplain forests, increasing knowledge about carbon accumulation and cycling in floodplain forests, and contributing to global carbon assessments.

**Keywords:** productivity; herb layer; seasonality; diffusive non-interceptance; riverine; forbs; soil temperature

## 1. Introduction

Floodplain forests are one of the most threatened types of azonal vegetation worldwide [1,2]. Their structure and functioning are strongly driven by the characteristics of river valleys. River flow influences distribution of species and creates successional gradients across the floodplain: pioneer ruderal species colonize river banks, while late-successional species (more competitive and prone to disturbance) occur on the slopes [3,4]. River regulation destroys the equilibrium between disturbances and succession, shaping the diversity of ecosystem types within the riverine area [1,2,5].

This phenomenon can lead to biotic homogenization of floodplain vegetation through the extirpation of specialized species, which are replaced by cosmopolitan species [6–8], as well as to increasing risk of biological invasions [4,9,10].

In cities, floodplain ecosystems, as well as wetlands and acidophilous forests, are one of the most endangered habitat types [11–13]. Thus, one of the most severe threats to floodplain forests is urbanization. Floodplain forest habitats close to settlements are usually cut for fuel and construction materials [2,5,14]. Moreover, urbanization can cause a lowering of the ground water table, increasing nitrogen deposition, pH, pollution and temperature [15–17]. Additionally, affinity of urban green areas and land-use change increases risk of invasive species encroachment [18–20].

Although understory comprises circa 1% of forest ecosystem biomass [21], due to seasonal dynamics, it is responsible for circa 20% of micro- and macroelement cycling [22–24]. Moreover, understory is much richer in plant species than overstory. Seasonality of deciduous forest ecosystems is connected with foliage fall during the autumn and its emergence during spring [24–26]. These dynamics imply taxonomic and functional diversity of dominants in understory biomass [26–28]. Seasonal dynamics are driven by changes in canopy openness, which allow development of spring ephemerals during an early spring period of high light availability, followed by decreasing light availability during late spring and summer [29,30]. Another factor connected with seasonal variability is temperature [26,31,32]. Additionally, understory biomass is driven by overstory characteristics [33,34] such as the dominant tree species [35–37]. Moreover, it is also driven by the temperature [38]. Previous studies have described understory biomass crop as a whole pool [36,39,40], and only a few of them accounted for proportion of functional groups of plant species, e.g., [37,39,41].

In contrast to long-term [9,42,43] or spatial variability [5,44,45], patterns of seasonal dynamics of understory species composition and biomass in riparian forest is largely unknown. Our literature review in Web of Science (string "((((("biomass" AND (((understor* OR "herb layer")) OR "herbaceous")) AND ((dynami* OR season*) OR "time seri*"))) AND ((riparian OR riverine) OR floodplain)))" searched 23 May 2018) revealed 111 studies. Some studies revealed interesting information about herbaceous plant decomposition [46] or biomass of non-forest vegetation [47,48] or forest vegetation [40,49]. However, only two studies focused on the seasonal dynamics of herbaceous biomass. Mabry et al. [50] assessed differences in floodplain forest understory at only two dates (spring versus summer) and Dunham [51] assessed biomass dynamics of perennial grasslands in the Zambezi floodplain woodland. Moreover, some authors studied biomass seasonality of individual understory plant species [26,41,52]. Therefore, there is no information about full seasonal dynamics of understory biomass in temperate zone floodplain forests. Thus, we aimed to assess seasonal dynamics of biomass and species composition of understory vegetation in degraded and non-degraded floodplain forests, to improve our understanding of carbon pools and biodiversity in forest ecosystems. We hypothesized that a degraded and non-degraded floodplain forest will differ in its pattern of seasonal variability of biomass and species composition [49], due to former usage, presence of alien species and differences in tree stand composition [25,36,38]. We also hypothesized that temperature and light availability drive biomass production and species composition.

## 2. Materials and Methods

### 2.1. Study Area

The study was conducted in a floodplain forest of the Warta River Valley in Poznań (W Poland, 52°24′ N; 16°57′ E). The climate of Poznań is transitional between maritime and continental with mean annual temperature of 8.4 °C and mean annual precipitation of 521 mm for 1951–2010 [53]. Typical vegetation types in floodplain forests are chracterized by *Salix alba* L. and *S. fragilis* L. (*Salicetum albae*), with *Populus alba* L. (*Populetum albae*), with *Ulmus minor* Mill. and *Quercus robur* L. (*Querco-Ulmetum minoris*). Floodplain forests occur in a complex mosaic with deciduous forests dominated by *Q. robur*, *Tilia cordata* Mill. and *Carpinus betulus* L. (*Galio sylvatici-Carpinetum*), as well as *Pinus sylvestris* L.

plantations and stands of invasive *Acer negundo* L. Non-forest vegetation types occur in the form of meadows, reeds and grasslands [4,54].

We undertook our study in floodplain forest dominated by *Q. robur* and *U. minor* (*Querco-Ulmetum minoris*). This type of floodplain forest usually occurs along the slopes of the river valley that are not frequently flooded (less than once per decade). The tree canopy is dominated by *Q. robur* and *U. minor* and the understory is composed of species typical to both floodplain forests and non-flooded hardwood forests [55]. We conducted field reconnaissance in the study area to locate two potential study plots (Figure S1). The criteria for study plots were understory homogeneity, an area of at least 1000 $m^2$ to provide a representative area for at least 20 sampling dates without double sampling of the same point and a buffer zone to prevent edge effects (if possible). The number of sample plots was limited by the high labor demand for sampling during the first dates (i.e., 10 h for each of 10 people for both plots). Although the low number of plots (two) does not meet the criteria for spatial replicability, our study provides unique insight into seasonal dynamics of understory biomass via quantitative assessment of biomass throughout the growing season. Also other studies conducted in single sites may provide an unique opportunities for studying time series of biological phenomena, such as wood increments, phenology or functional traits variability (e.g., [26,56,57]). We are conscious that our conclusions are limited to the study area and extrapolation of our findings to other floodplain forests is limited; however, the temporal nature of our study could provide insights understanding short-term plant community dynamics and the influence of disturbance on them in floodplain forests in the region.

We established two study plots: degraded (20 m × 60 m) and non-degraded (30 m × 65 m). Borders of the study plots were marked at the time of the study. The study plots differ in distance to the river valley (though both are rarely under impact of the river; Figure S1) and vegetation structure (Table S1). The degraded plot was characterized by a higher proportion of alien species in both overstory and understory, higher proportions of cosmopolitan and forest edge species in the understory, lower canopy closure and higher proportion of alien species, both in overstory and understory. The classification of plots as degraded or non-degraded plots was based on vegetation surveys of riparian forests in the study area [4,54]. Tree stand basal area was 31.72 $m^2\ ha^{-1}$ in the degraded plot (dominants: *Q. robur* 59.3% and *Tilia cordata* + *T. platyphyllos* 22.3%) and 27.47 $m^2\ ha^{-1}$ in the non-degraded plot (dominants: *Ulmus* spp. 59.3% and *Q. robur* 38.1%; Figure S2). Both plots were located within the same soil type–alluvial soils, typical of river valleys. Mean topsoil pH (0–10 cm depth, five samples per plot) was 6.79 ± 0.34 in the degraded plot and 6.23 ± 0.09 in the non-degraded plot. Mean leaf litter masses, assumed as proxy for matter cycling rate [58], collected in April were 7056.57 ± 170.06 kg $ha^{-1}$ and 7788.82 ± 229.28 kg $ha^{-1}$, respectively.

### 2.2. Data Collection

We sampled aboveground biomass at 22 dates. At each date, from each plot, we collected 10 circular samples with an area of 0.16 $m^2$. The first harvest date was 19 March 2016, the last–26 November 2016. Due to rapid changes of understory vegetation during spring, the first eight harvests were conducted at weekly intervals, and further harvests were conducted every two weeks. In total, we collected 440 samples of understory biomass.

Sample locations were randomly selected by throwing a circular frame within the study plots. In cases where the frame landed on a previously sampled point, dense shrub layer or animal paths, we repeated the throw, to avoid impact of these factors. We harvested aboveground parts of all plants rooted within the frame. If a particular plant was partially within the frame, but the root was outside, the plant was not harvested. Using this method, we assumed that biomass of plants rooted outside the frame and partially covering the frame was equal to the biomass of plants rooted inside the frame and partially covering area outside the frame [27]. In cases of natural regeneration of trees and shrubs, we harvested only individuals <0.5 m height (assumed as a threshold between understory and shrub layer). Harvested plants were separated into species in the field, under supervision of the authors

(NC and MKD) and placed into paper envelopes. All specimens were dried in an oven with forced air circulation at 65 °C (ULE 600, Memmert GmbH + Co. KG, Schwabach, Germany), to a constant mass. Then, plant material was weighed using BP 210 S (Sartorius, Göttingen, Germany) scales, with an accuracy of 0.001 g. When the scale showed 0.000 g we assumed that the mass was 0.0005 g.

For forest floor temperature measurements, we used HOBO U23-001 (Onset Computer Corporation, Bourne, MA, USA) loggers, mounted at the soil surface in the center of each study plot. The loggers registered temperature each hour from 19 March 2016 to 26 November 2016 (Figure 1a). As a light availability proxy, we used a diffusive non-interceptance radiation measure (DIFN). At each study plot and each of the ten dates (Figure 1), we took six series of 20 measurements at randomly selected points. DIFN was measured using an LAI-2200 (Li-Cor Inc., Lincoln, NE, USA). In total, we measured DIFN 10 times, each second harvest of biomass (from 1 April 2016 to 26 November 2016; Figure 1b, Table S2). Then, for each harvest date, we interpolated DIFN as mean value of previous and next dates.

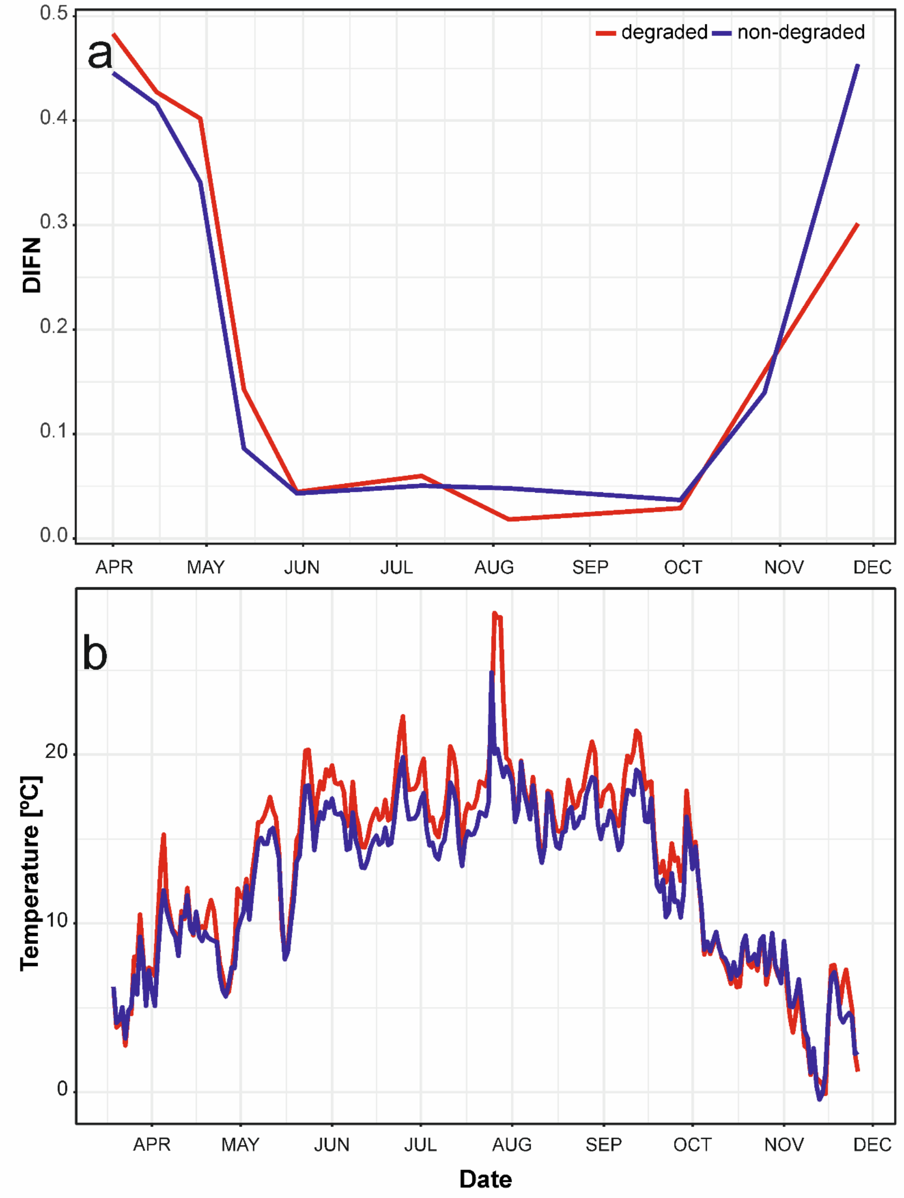

**Figure 1.** Mean daily temperatures of the forest floor within study plots (**a**) and mean DIFN (diffusive non-interceptance–fraction of the open sky) within study plots (**b**), measured for each two study plots on 10 dates (Table S2). APR, April; MAY, May; JUN, June; JUL, July; AUG, August; SEP, September; OCT, October; NOV, November; DEC, December.

### *2.3. Data Analysis*

For each plant species we determined their Ellenberg's ecological indicator values (EIV) [59] and life forms from BiolFlor [60]. EIVs describe species responses to ecological gradients using a nine-degree scale (with an exception of moisture which uses a 12-degree scale). An exception was *Glechoma hederacea* L., which we classified as hemicryptophyte because this species exhibited a hemicryptophyte life form in the study area rather than a geophyte (listed in BiolFlor). To assess differences of biomass crop between study plots, for each date we used *t*-tests, while differences among study dates were assessed using a generalized additive models (GAMs), using Julian day as an independent variable. GAMs were implemented in *mgcv::gam()* function [61]. We also used GAMs to assess influence of date on species richness. All mean values were followed by standard error (SE).

To analyze differences in species composition of understory biomass, we used a Detrended Correspondence Analysis (DCA). This analysis was used due to long environmental gradients (>3 standard deviations), which in cases of analyses assuming linear (PCA) or short unimodal (CA) gradients could generate artifacts (arch or horseshoe effects). A DCA was performed using the *vegan::decorana()* function [62]. DCA is a method of ordination of points representing species and sites within reduced space of species. Instead of large, species number-dimensions space, a DCA provides few axes expressing main dimensions of species composition change across samples. In our study, each sample was a species composition of understory biomass in particular date in particular plot. Using *vegan::envfit()*, we passively (not affecting species and site scores) fitted vectors representing proportion of main life strategies in biomass, weighted by species biomass EIVs and environmental parameters–DIFN and forest floor temperature. Statistical significance and coefficients of determination were assessed using a permutation test (999 iterations). These vectors show the direction of parameters changes within ordination space, i.e., whether points representing particular sites (i.e., plots and dates) had low or high values of a particular parameter. To assess the direct relationships between understory biomass, vegetation type (plot name), mean temperature of the previous two weeks before harvest and DIFN, we used linear regression. We assessed models using the Akaike Information Criterion to choose the most informative model. All analyses were conducted using R software [63].

## **3. Results**

### *3.1. Seasonal Dynamics of Biomass*

Our study revealed statistically significant differences both among study dates and study plots (Table S3; Figure 2). Collection date explained 32.5% and 35.7% of variance, in non-degraded (estimated degree of freedom = 5.19, F = 16.85, $p < 0.001$) and degraded plots (estimated degree of freedom = 6.79, F = 15.66, $p < 0.001$), respectively. Mean aboveground biomass of understory in the degraded plot was 444.73 ± 10.54 kg $\text{ha}^{-1}$ and was higher than biomass of the non-degraded plot (398.48 ± 9.32 kg $\text{ha}^{-1}$). In the degraded plot, the highest biomass crop was on 24 April (930.12 ± 48.70 kg $\text{ha}^{-1}$) and the lowest was on 26 November (74.85 ± 4.83 kg $\text{ha}^{-1}$). In the non-degraded plot, we found the highest biomass crop on 30 May (768.99 ± 40.65 kg $\text{ha}^{-1}$) and the lowest on 19 March (80.92 ± 3.14 kg $\text{ha}^{-1}$). Culmination of biomass crop in the non-degraded plot was 35 days later than in degraded plot.

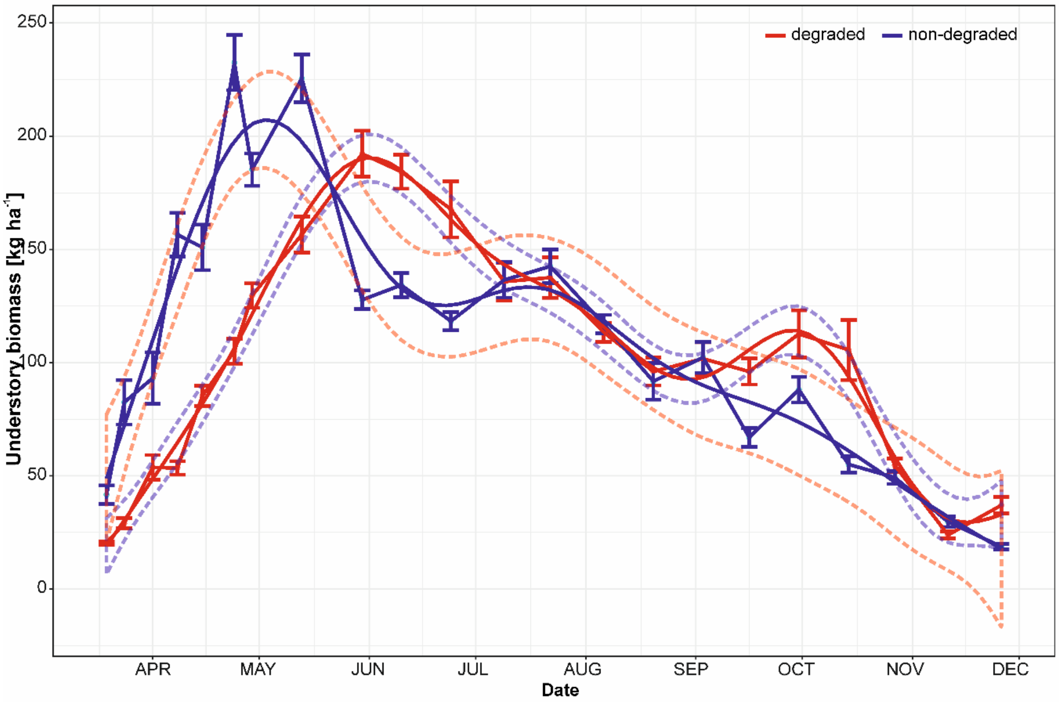

**Figure 2.** Changes of understory biomass (mean ± SE) across the growing season 2016 and GAMs showing relationship between biomass and date (dashed lines represent the range of model SE).

### 3.2. Dynamics of Species Richness

During the whole study we found 78 plant species (including 56 herbaceous and 23 woody species). At the single sample level (0.16 m$^2$) species richness ranged from 2 to 19 species (Figure S3). However, only a few species occurred at high frequency (>40% of samples): *Chaerophyllum temulentum* L. (found in 283 samples), *Alliaria petiolata* L. (280), *Impatiens parviflora* DC. (239), *Glechoma hederacea* (179), and *Viola odorata* L. (178). The largest differences in species richness was found in the degraded plot on 15 April 2016: species richness ranged from 7 to 17. The lowest richness was on 26 October: from 3 to 5 species. Mean species richness per sample was 8.84 ± 0.02. In the non-degraded plot we found the highest variability of species richness per sample on 13 May (5 to 15 species), and the lowest on 19 March (4 to 6 species) and on 11 November (2 to 4 species). Mean species richness per sample was 5.99 ± 0.01. Analyzing species richness for all samples from each date, we found that mean species richness in the degraded plot was 21.31 ± 0.22 and in non-degraded—19.23 ± 0.29 (Figure 3). Species richness in the degraded plot ranged from 12 (11 November) to 29 (24 April) and in the non-degraded plot–from 9 (26 November) to 33 (13 May). In both plots we confirmed statistically significant change of species richness over time with peaks at the spring. However, the peak was more clear in degraded (estimated degree of freedom = 5.29, F = 9.37, $p < 0.001$, $R^2 = 0.74$) than non-degraded plot (estimated degree of freedom = 3.86, F = 4.28, $p = 0.011$, $R^2 = 0.47$).

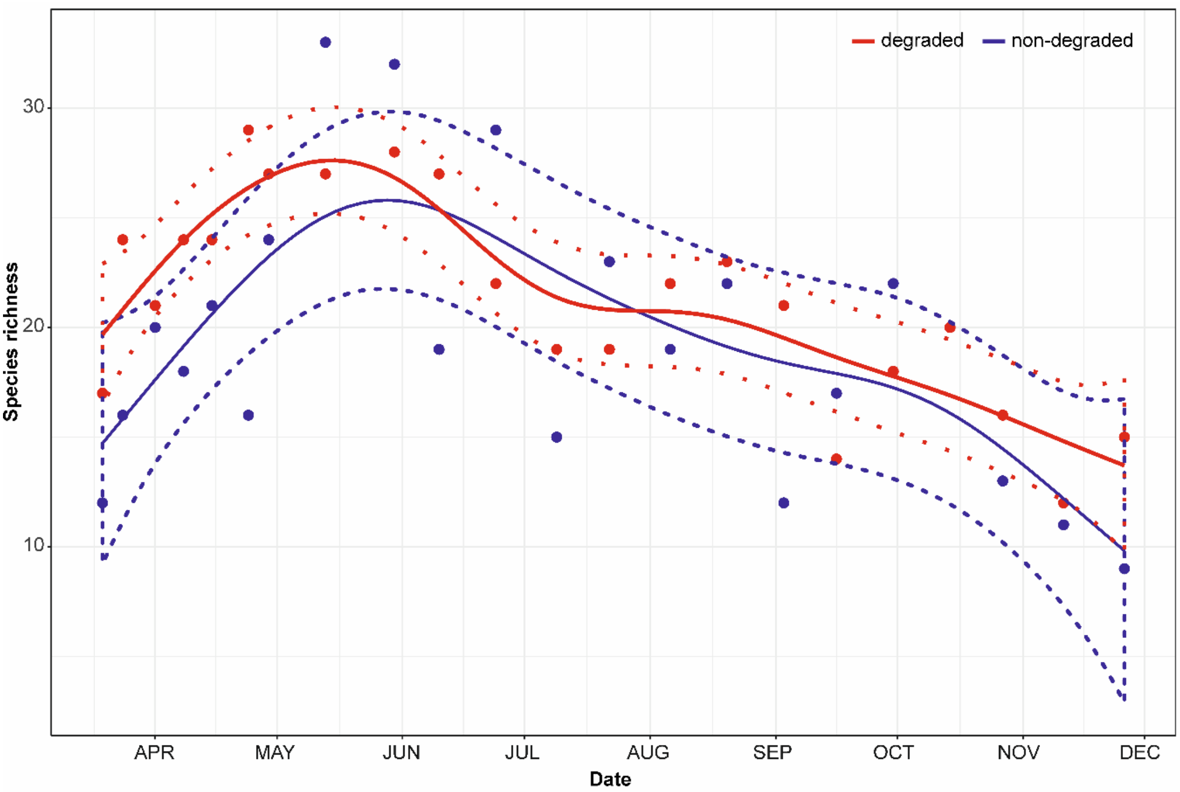

**Figure 3.** Change of species richness per plot for each study date and GAMs showing relationship between biomass and date (dashed lines represent the range of model SE).

### *3.3. Dynamics of Life Form Proportions*

At the beginning of the study (19 March; Figure 4), we found the highest proportion of phanerophytes (51%) and geophytes (23%) in the degraded plot. From 24 March to 29 April geophytes comprised over 45% of aboveground biomass in the understory with the proportion of therophytes increasing until August where they comprised 30% of plant biomass. The proportion of phanerophytes ranged from 9% (15 April) to 51% (19 March). The proportion of hemicryptophytes increased from 30% on 24 June reaching 68% on 14 October (Figure 4).

In the non-degraded plot at the beginning of the study (19 March) proportions among all life forms groups (phanerophytes, geophytes, hemicryptophytes, therophytes) ranged from 15% to 25%. At the first three dates (up to 1 April), we noticed an increase in proportion of geophytes from 23% to 54%. Then, on 24 April it was slightly over 40% and started decreasing. Maximal proportion of phanerophytes reached 26% (26 November) and that for therophytes was 21% (10 June). Understory biomass was dominated by hemicryptophytes, the proportion of which exceeded 30% from 24 April until the end of the study. Their highest proportion occurred on 14 October (84%). From 30 May to 11 November hemicryptophytes compromised over 50% of understory biomass.

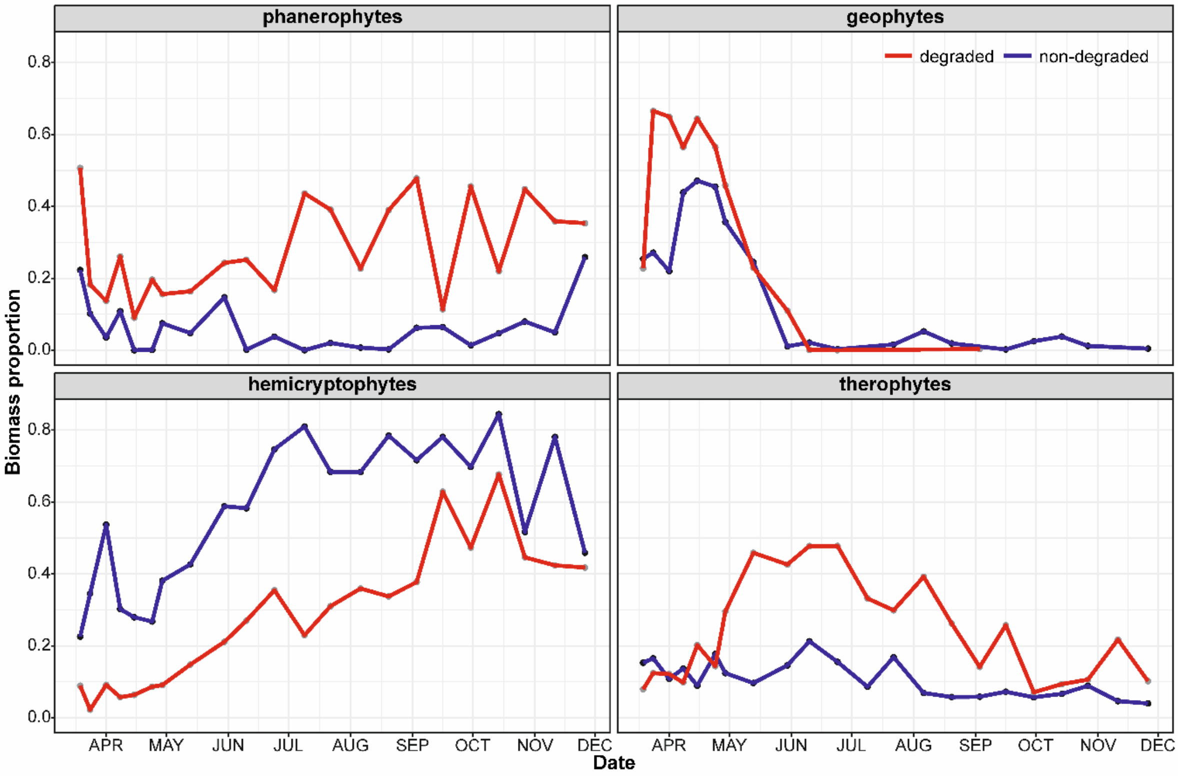

**Figure 4.** Proportion of biomass of species from life strategies: phanerophytes (woody species > 0.5 m height), geophytes (perennial species with regeneration buds belowground), hemicryptophytes (perennial species with regeneration buds at the ground level) and therophytes (annual species).

### 3.4. *Impact of Environmental Factors on Understory Biomass Species Composition Dynamics.*

The DCA revealed that environmental factors influenced understory biomass species composition and seasonal dynamics in each plot differently (Figure 5, Table 1). The two plots were strongly separated in ordination space; the main direction of compositional shifts during the growing season in degraded plots followed the DCA1 axis, i.e., points representing earlier dates were located in lower part of the DCA space while later dates were located in higher parts. In contrast, changes in the non-degraded plot understory followed the DCA2 axis. However, in both plots, points representing the first and last dates were closer than points representing intermediate dates. The vector representing proportion of phanerophytes was directed into the part of ordination space occupied by the degraded plot, where its proportion was higher than in the non-degraded plot, similar to vectors representing proportions of alien species and therophytes. The vector representing moisture EIV was directed into the ordination space occupied by the non-degraded plot, indicating higher values of moisture EIV. Vectors representing day of year, proportion of hemicryptophytes, species richness, DIFN and proportion of geophytes were directed along the DCA2 axis, indicating the seasonal dynamic within both plots. We found that DCA2 axis was negatively correlated with vectors representing species richness, DIFN and proportion of geophytes, while positively with Julian day of the year and proportion of hemicryptophytes.

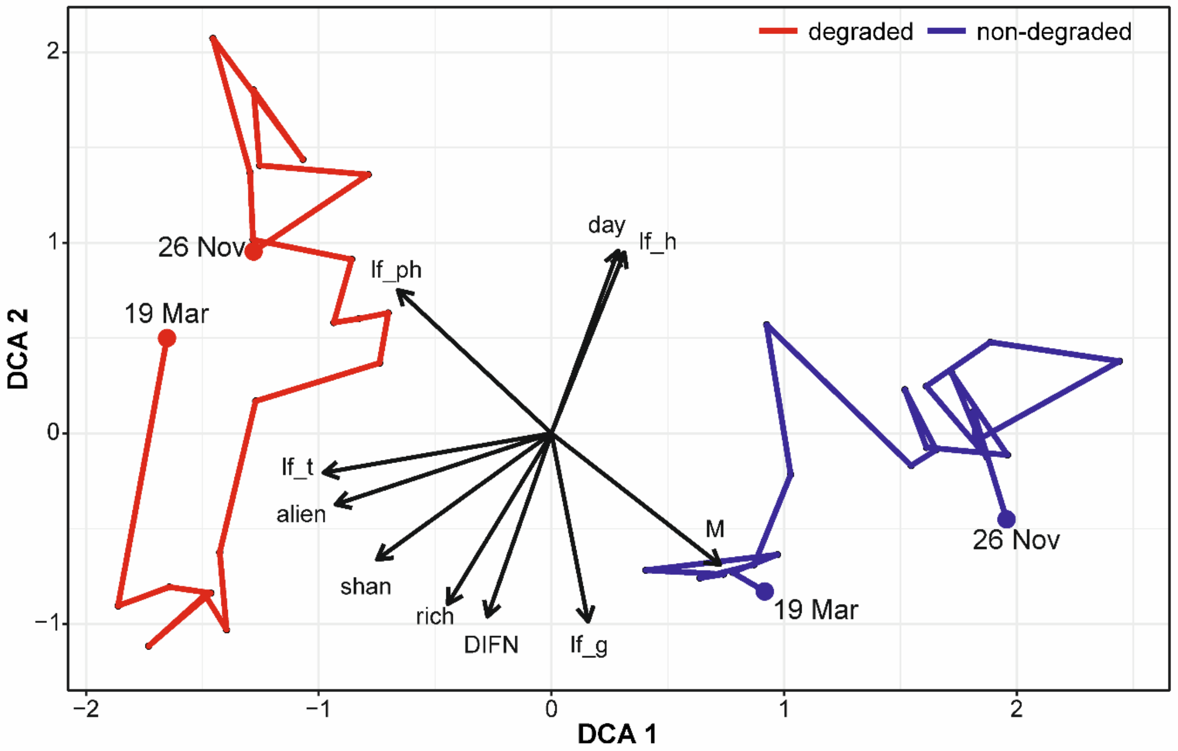

**Figure 5.** Result of Detrended Correspondence Analysis (DCA) for each study plot and study date. Each point represents pooled biomass from 10 samples. The big dots represent the first and last harvest, and the lines subsequent harvest dates. Eigenvalues: DCA1 = 0.7204, DCA2 = 0.3935. Abbreviations and fitting parameters of vectors are given in Table 1.

**Table 1.** Parameters of environmental variables fitted to the DCA analysis.

| Parameter | Abbreviation | DCA1 | DCA2 | $R^2$ | $p$ |
|---|---|---|---|---|---|
| Day in year | day | 0.28602 | 0.95822 | 0.6060 | 0.001 |
| Temperature | temp | 0.07346 | 0.99730 | 0.1524 | 0.065 |
| DIFN | DIFN | −0.27537 | −0.96134 | 0.4247 | 0.001 |
| Proportion of life forms | | | | | |
| - phanerophytes | lf_ph | −0.65970 | 0.75153 | 0.6717 | 0.001 |
| - geophytes | lf_g | 0.15727 | −0.98756 | 0.7070 | 0.001 |
| - hemicryptophytes | lf_h | 0.31312 | 0.94971 | 0.7278 | 0.001 |
| - therophytes | lf_t | −0.97844 | −0.20653 | 0.3683 | 0.002 |
| Ellennberg’s ecological indicator values | | | | | |
| - soil fertility | N | 0.74511 | 0.66694 | 0.0876 | 0.216 |
| - moisture | M | 0.72399 | −0.68981 | 0.6979 | 0.001 |
| - soil reaction | SR | 0.27500 | −0.96144 | 0.0473 | 0.466 |
| Shannon diversity index | shan | −0.74938 | −0.66214 | 0.4589 | 0.001 |
| Species richness | rich | −0.44518 | −0.89544 | 0.2129 | 0.023 |
| Proportion of alien species | alien | −0.92770 | −0.37331 | 0.3378 | 0.002 |

An analysis of temperature and DIFN impacts on biomass revealed a quadratic relationship with DIFN and linear relationship with temperature of the last two weeks ($R^2$ = 0.248; Table 2). Type of vegetation (difference between study plots) was not included in the final model.

**Table 2.** Linear regression model of understory biomass.

| Parameter | Estimate | SE | *t* Value | Pr (>\|t\|) |
|---|---|---|---|---|
| (Intercept) | −349.930 | 241.110 | −1.451 | 0.155 |
| mean temperature of previous two weeks | 43.860 | 12.190 | 3.597 | 0.001 |
| DIFN$^2$ | −5155.920 | 2373.290 | −2.172 | 0.036 |
| DIFN | 3158.170 | 1322.740 | 2.388 | 0.022 |

AIC = 563.001; AIC of null model (intercept-only) = 601.502, $R^2$ = 0.248.

## 4. Discussion

### 4.1. Limitations of the Study

Our study seemed to suffer from a lack of replicability–each forest type was represented only by one large study plot, where subsamples were randomly selected. However, numerous studies based on only one study site often provide unique results, which are crucial for further studies. Such examples are phenological observations, tree ring research or detail spatial analyses of forest structures (e.g., [56,57,64]). Although it is not possible to infer results for all floodplain forests, even floodplain forests representing the *Querco-Ulmetum minoris* plant association. Potential replication treatments would need to cover forests with similar light availability and tree stand species composition, as well as distance from river and elevation. Lower number of samples could be applied to increase the number of study plots. In our opinion, if one expanded the number of plots, one could decrease the number of samples to six. On the other hand, biomass dynamics studies demand high amounts of labor in both the field and the lab. For that reason, other studies are also usually limited in number of plots, e.g., [50] with eight 0.25 m$^2$ plots at two dates. Another sampling limitation is a necessity for a large homogenous area, which allows for both random sampling at each date, as well as preventing edge effects and random disturbances. Despite these drawbacks, according to our knowledge and searched literature data, we provided the first data about seasonal dynamics of biomass in floodplain forests.

### 4.2. Biomass Crop and Its Change over Growing Season

Our study revealed differences between study dates and study plots. Previous studies on dynamics of biomass production usually confirmed this effect [27,28], however, see [41] for an exception. In our study, the culmination of understory biomass crop lasted from the end of April to the end of June, despite compositional shifts. This indicates the high rate of matter cycling [23,24]. Additionally, other studies reported high biomass crops in floodplain ecosystems. For example, riparian forests in northern France and Belgium had median biomass of 80–90 kg ha$^{-1}$ [65], which did not differ along a flooding gradient. Canadian floodplain forest summer understory biomass varied among tree stand types and ranged from 2640 (beneath *Betula populifolia* Marsch.) to 30 kg ha$^{-1}$ (beneath *Thuja occidentalis* L.) [36]. In a *Quercus alba* L. and *Q. rubra* L. floodplain forest in Iowa, USA, spring and summer biomasses were 600.0 and 981.2 kg ha$^{-1}$, respectively, whereas in a *Celtis occidentalis* L. -*Juglans nigra* L. -*Prunus serotina* Ehrh. forest they were 228.8 and 241.2 kg ha$^{-1}$, respectively [50]. In the Sierra Madre mountains (Wyoming, WY, USA), herbaceous understory biomass ranged from 0.4 to 2 kg ha$^{-1}$ [40]. In an Amazonia riparian forest, understory biomass was estimated at 400–1800 kg C ha$^{-1}$ [49], which, assuming carbon content of 50% of biomass, corresponded to 800–3600 kg ha$^{-1}$. Thus, the mean biomass of understory provided by our study is comparable with other studies on riparian forests understory biomass worldwide. For comparison, deciduous forests from European countries (including alluvial forests) varied in understory biomass from 1 to 2868 kg ha$^{-1}$, depending on soil pH and tree layer cover [38].

Other studies describing seasonal dynamics also showed an increases in herbaceous biomass in the spring. Tremblay and Larocque [41] found low seasonal dynamics of understory biomass in four types of forests. However, this resulted from high proportions of woody species in biomass in the cited study. Seasonal dynamics of biomass revealed by us resembled those of hardwood forests with *Quercus robur*, *Carpinus betulus* and *Tilia cordata* [27,28]. These dynamics were driven by both different dates of particular species emergence, as well as different seasonal dynamics of biomass production [26,30,41]. The latter is also connected with increasing foliage efficiency (higher specific leaf area) when light availability decreases [26]. Additionally, Axmanová et al. [38] revealed a negative correlation between light availability and understory biomass. However, they used cover of the tree layer (estimated visually) instead of direct measurements.

### 4.3. Differences between Non-Degraded and Degraded Floodplain Forest

Our study revealed different compositional trajectories of understory biomass of degraded and non-degraded floodplain forests. This is similar to Mabry et al. [50], who found almost three times more differences in aboveground understory biomass between intact (higher biomass) and disturbed floodplain forests in spring. However, these differences in summer were low and statistically insignificant. In the cited study, higher spring biomass in the intact site was caused by the presence of spring ephemerals. In our study, these plants were more present in the degraded forest. This was also affected by the presence of *Eranthis hyemalis* Salisb.–a naturalized geophyte reaching high biomass in March and April.

Differences in understory biomass between the forests studied (degraded versus non-degraded) resulted from different species composition, which is driven by tree species. Different tree species create different light availability [66], which also affects soil temperature and transpiration [31,67]. *Ulmus* spp. Especially, contributed to shading as they have a high leaf area index [62], which results in lower light availability in the non-degraded forest (Figure 2). Despite the presence of shading, *Tilia* spp. and *Acer* spp. in the degraded plot, lower canopy closure (Figure S2), caused higher light availability. Tree species effects on understory biomass were also noted by other studies [36,38,41].

### 4.4. Dynamics of Life-Forms Proportions

Similar to our results, a study from Canadian forests [41] showed more or less constant proportions of woody species in understory biomass. This may be connected with high emergence of seedlings with low individual biomass and high mortality in spring [58]. The highest proportion of phanerophytes at the beginning of our study may have resulted from the emergence of high number of woody species seedlings.

The main source of variation in biomass was connected to the seasonal dynamics of the geophytes (mostly spring ephemerals). This group is an important driver of biomass in other fertile broadleaved forests. For example, in Małopolska (S Poland), the maximum understory biomass in a *Quercus-Carpinus-Tilia* forest with geophytes reached up to 660 kg $\text{ha}^{-1}$, whereas in *Fagus sylvatica* forests without geophytes, it only reached 49 kg $\text{ha}^{-1}$ [68]. This impact was also noted by other authors [27,28,41]. The impact of therophytes was connected mainly with the occurrence of invasive *Impatiens parviflora*, which is the most frequent alien species in European forests [69–71]. This species reached the highest individual biomass between spring and summer [72,73].

## 5. Conclusions

Our study revealed highly dynamic species composition and biomass of understory vegetation in floodplain forests over the course of the growing season. However, the amount of biomass was more or less constant across the peak of the growing season, with larger changes occurring at the beginning and end of the growing season. At the start of spring ephemerals contributed to high biomass pool, however, this was a transient peak in biomass that did not persist across the growing season. This dynamic influenced species composition shifts and small differences in biomass crop between constitutive dates. Additionally, we found differences in patterns of understory biomass dynamics between degraded and non-degraded plots, connected with the lower proportion of spring ephemerals and therophytes in the latter. The main understory biomass components comprised spring ephemerals (mainly geophytes) contributing to quick biomass increments during spring and species present during the whole season (mainly hemicryptophytes and woody species). We also quantified the impacts of light availability and temperature on understory primary production. Biomass crops increased with increasing light availability and temperature. Light availability also influenced species composition.

Although the inferences that can be made are limited due to the study design, they provide a novel and important insight into understory primary production. Accounting for limitations in inference, we may conclude that changes in understory biomass of floodplain forests are rapid and contribute strongly to matter cycling in these ecosystems. For that reason, our study increased the knowledge about carbon accumulation and cycling in floodplain forests [26,40,74]. The degradation influences the pattern studied by alteration of understory species composition, especially proportion of functional guilds.

**Supplementary Materials:** The following are available online at http://www.mdpi.com/1999-4907/10/1/22/s1. Figure S1: Locality of the study plots: a. locality at the background of satellite imaginary, b. locality of study plots at the background of the borders of Poznań city (W Poland; 52°24′ N; 16°57′ E). Plot no. 1–degraded floodplain forest, plot no. 2–non-degraded floodplain forest. Figure S2: Tree stand species composition–basal area of particular tree species in tree stand layer (trees > 7 cm diameter at breast height). Figure S3: Boxplots representing species richness per sample (10 samples per date). Box represents interquartile range, bar inside box–median, whiskers–range of minimum and maximum excluding outliers (points). Table S1: Phytosociological table for degraded and non-degraded floodplain forests at two dates and conducted in three 100 $m^2$ subplots per study plot. Plant communities represent the *Querco-Ulmetum minoris* association. Table S2: Seasonal variation in DIFN among 22 dates and between plots. Differences among terms within each plot were assessed using one-way ANOVA (dates marked with the same letters did not differ statistically significantly at $p = 0.05$). Differences between study plots within the same date were assessed using *t*-test. Table S3: Seasonal variation in understory biomass (Mean ± SE biomass (kg/ha)) among 22 dates and between plots. Differences between study plots within the same date were assessed using t-test. Response variable was log transformed prior to analyses.

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