Shifts in Riparian Plant Life Forms Following Flow Regulation

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Abstract: Flow regulation affects bordering riparian plant communities worldwide, but how different plant life forms are affected by river regulation still needs further research. In northern Sweden, we selected 10 rivers ranging from free-flowing to low, moderately, and highly regulated ones. In 94 reaches across those rivers, we evaluated the relative abundance of woody and herbaceous (i.e., graminoids and forbs) life forms, their species richness, and their relative presence. We also explored which, and to what extent, hydrological variables drove species assembly within each life form. The relative abundance and species richness of each life form decreased across river categories with increasing levels of regulation. This was particularly apparent in herbaceous life forms, and the most drastic decreases were observed in all life forms in moderately or highly regulated reaches. Additionally, when river regulation increased, the relative presence of many species from all life forms decreased. Unlike woody species, only a few new herbaceous species appeared in regulated reaches. A canonical correspondence analyses (CCA) revealed that a wide range of hydrological variables explained the occurrence of woody species, while fewer variables explained variation in the graminoid and forb life forms. We conclude that flow regulation and its intensity result into clear shifts in the relative abundance of different life forms, as well as in changes of within-group species richness and composition. Consequently, the modification of certain flow attributes in flow regulation schemes, as well as the intensity of these modifications, may alter the ratio between herbaceous and woody species, ultimately impacting the functions and benefits derived from each life form.

Keywords: forb; functional group; graminoid; hydrological variable; vegetation; woody

1. Introduction

It is obvious that changed flow regimes affect plant growth, performance, and distributions [1,2]. However, since studies on many species at once are relatively scarce or restricted to smaller spatial scales, many questions about community responses are still unanswered. This is unfortunate, as general frameworks (as opposed to species-specific or site-specific frameworks) are essential to develop flow management guidelines for regional or national water management plans. To overcome the difficulties of working at a species level, classification into functional groups has been advocated and used in other ecological theories [3]. Functional groups include species sharing certain traits, resulting in common

habitat requirements and responses to environmental changes. Despite the growing number of studies using functional groups, they remain somewhat controversial because they depend on which traits have been considered, especially when classification is limited by the information that is available in trait databases [4].

Plant life form schemes are widely accepted functional groups (first conceived by the authors of [5]). A plant life form is defined as the structural form of a plant in its typical or preferred habitat. The simplest life form classification separates woody and herbaceous species. Other more complex classifications have developed within these two categories and are well known [6–8]. Despite these being very broad groups, species within each life form bear enough similarities when dealing with broad or general questions on community structure. For instance, life span separates long-lived woody species from more frequently annual herbaceous species, and it allows for the generalization of, for instance, community turnover. Additionally, stature and associated plant height separate tall woody species from shorter graminoid and forb species, resulting in clear differences in resource acquisition between life forms. Propagation, seasonal growth habits, and protective structures are other characteristics that separate those life forms that allow for the generalization of the community processes based on them. To balance between generalization and detail, sub categories are distinguished (e.g., trees, shrubs, sedges, grasses, legumes, clonal and non-clonal forbs).

Because plant life forms reflects a plant's adaptation to its environment, it also has consequences for the response to disturbance [9]. A large body of literature has documented life form-specific responses to changed climatic factors [10], increased anthropogenic pressure [11], fire [12], and water shortage [13], among others. Flow regulation serves different purposes (e.g., irrigation, water supply, and hydropower generation) and has been shown to promote or disfavor certain species and, ultimately, whole functional groups depending on what species traits are favored by the new conditions [14–16]. However, flow regulation includes many specific changes in the flow regime (e.g., flooding frequency, flooding duration, and flooding timing), each of them with differing ecological implications [17].

Shifts in the relative abundance of different life forms may or may not result in shifts in species and functional diversities. The maintenance of functional diversity can guarantee the continuation of important ecosystem processes and functions despite decreased species numbers [18]. Therefore, changes in flow regime are expected to induce larger changes in riparian communities when the functional diversity, rather than the absolute species diversity, is affected. A simple classification of riparian plants into few different life forms could enable a straightforward visual evaluation of riparian plant communities and their susceptibility to flow regulation and associated ecological consequences.

In this study, we used flow attributes to characterize a wide range of flow regulation regimes and tested the effects of flow regulation on the relative abundance of woody and herbaceous (i.e., graminoids and forbs) life forms, their species richness, and their relative presence across large spatial scales. We hypothesized that (i) certain life forms contain more plant species that are sensitive to flow regulation. Because of that, flow regulation (ii) will affect that particular life form more strongly than other life forms, eventually removing such life form from the riparian community, along with an associated loss of functional diversity. Finally, because species within woody and herbaceous life forms exhibit specific traits that interact differently with hydrological regimes, we hypothesized that (iii) different hydrological variables drive species within that functional group.

2. Material and Methods

2.1. Study Area and Data Collection

The study area in northern Sweden comprises 205,764 km^2 and is dominated by boreal coniferous forest (Figure 1). The study reaches were selected along 10 rivers within nine basins: Torne, Kalix, Sävarån, Vindel, Öre, Pite, Lule, Skellefte, Ume, and Ångerman (Figure 1). The rivers run from the Norwegian border and end at the Gulf of Bothnia, except for the Vindel River that joins the Ume River 35 km from the coast. Most rivers are large (i.e., a channel length

between 360 and 510 km, a catchment area between 11,285 and 40,157 km^2, and a mean monthly discharge between 131 and 501 m^3/s), except for the Sävarån and Öre rivers, which are smaller (128–185 km, 3029–1160 km^2, and 34–15 m ^{3}/s, respectively). Some rivers have no major dams and may be considered free-flowing (Torne, Kalix, Sävarån, Vindel, and Öre), whereas others are regulated by one to several dams and are considered moderately-to-strongly regulated rivers (Pite, Lule, Skellefte, Ume, and Ångerman). Despite river specific differences, the upland vegetation (furthest away from the channel) is generally characterized by birch (*Betula pubescens* Ehrh.) and coniferous forests (*Pinus sylvestris* L. and *Picea abies* (L.) H. Karst.). The riparian vegetation closer to the river channel frequently includes woody species like *Alnus incana* (L.) Moench, *Betula pubescens*, and *Salix* spp.; graminoids like *Carex* sp.　and *Poa* sp.; and forbs like *Ranunculus reptans* L. and *Filipendula ulmaria* (L.) Maxim.
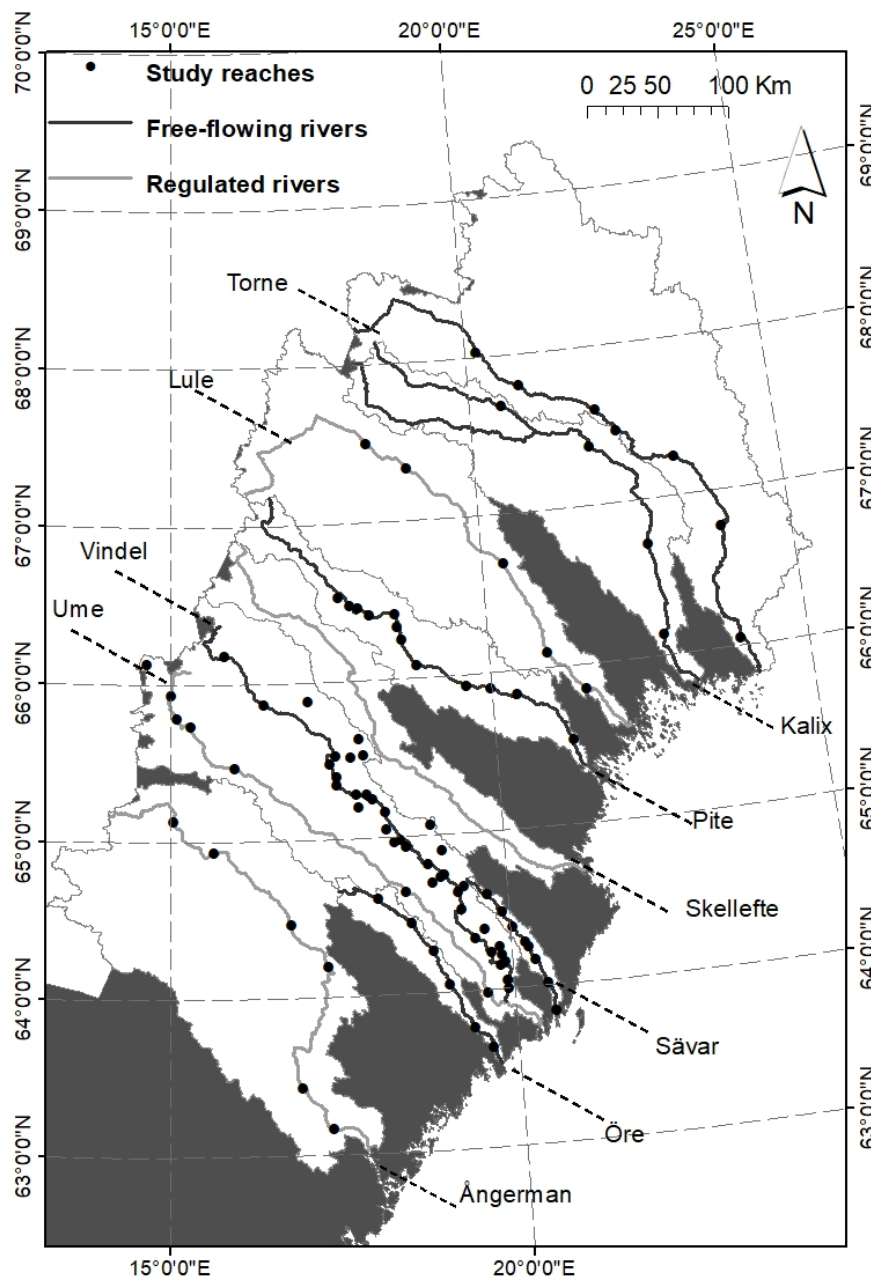

Figure 1. Selected reaches along the 10 river basins in northern Sweden. Black lines are free-flowing rivers, and grey lines are regulated rivers. Dots represent the 94 study reaches, and lines represent the course of the main channels of the rivers.

We obtained hydrological and floristic data from 94 reaches across 10 rivers from [16], as available in the Dryad repository [19]. The hydrological data consisted of 16 variables that characterize ecologically relevant facets of the annual hydrograph at a reach scale (e.g., the magnitude, timing, duration, frequency, and rates of change of the flows; Table 1 and Annex 1). As an overall measure of the degree of regulation, we calculated the percentage of the natural mean annual discharge potentially stored in reservoirs upstream from the reach. Based on the degree of regulation, we categorized reaches into free-flowing (<0%; $n = 63$) and with a low (>0% and <15%; $n = 14$), moderate (>15% and <60%; $n = 8$), and high (>60%; $n = 9$) degree of regulation. The floristic data of each reach consisted of plant species' presence–absence, as recorded along a 200 m long section by the Landscape Ecology research group (Umeå University, Sweden) (Annex 2). Species were classified into the simplest life form groups: woody, graminoid, and forb species. The few number of woody species compared to the herbaceous ones prevented us from subdividing this group into trees and shrubs. Conversely, the large number of herbaceous species led us to subdivide them into graminoids and forbs. For the sake of simplicity, we discarded other more complex groupings (e.g., [6]). Hydrological series were either recorded (the longest from 1909 and the shortest from 1988) or modeled (when no recorded data were available; from 1999 to 2011). Floristic data were collected during the nineties by the Landscape Ecology Group at Umeå University. The reader is referred to the [16] for more details on the dataset.

Table 1. Mean and standard deviation of the hydrological variables characterizing each flow regulation group. "*n*" indicates the number of sites included within each flow regulation group. Letters "a," "b," "c," and "d" identify significant differences between groups ($p < 0.05$), while the trend across groups is indicated with an arrow.

Hydrological Variable	Free-flowing ($n = 63$)		Low ($n = 14$)		Medium ($n = 8$)		High ($n = 9$)		Trend
	Mean	Std. Deviation	Mean	Std. Deviation	Mean	Std. Deviation	Mean	Std. Deviation	
Reg	0.00 [a]	0.00	6.71 [b]	2.20	39.99 [c]	7.34	84.48 [d]	18.07	↗
MMaxMst	3.07 [a]	0.46	2.48 [b]	0.32	1.39 [c]	0.35	1.37 [c]	0.18	↘
MMinMst	0.21 [a]	0.08	0.30 [b]	0.07	0.68 [c]	0.21	0.51[c]	0.23	↗
MT2st	5.47 [a]	1.52	3.33[b]	0.58	2.62 [c]	0.57	1.95 [d]	0.26	↘
TMaxM	1.52 [a]	0.62	2.00 [b]	0.00	3.29 [b]	3.24	8.39 [c]	2.47	↗
TMinM	10.86 [a]	0.66	11.86 [b]	0.53	8.25 [a]	5.20	4.56 [c]	4.61	↘
TXLow	293.69 [a]	112.21	298.93 [a]	103.72	106.89 [b]	94.62	89.13 [b]	83.61	↘
TT2	32.37 [a]	15.26	61.67 [b]	17.47	100.12 [c]	27.30	152.77 [d]	78.36	↗
DMaxM	1.32 [a]	0.52	1.71 [b]	0.47	5.31 [c]	4.25	6.83 [c]	3.14	↗
DMinM	1.86 [a]	0.50	1.86 [a]	0.36	3.38 [a]	2.92	2.78 [a]	2.82	↘
DXLow	37.65 [a]	13.43	13.30 [b,c]	16.38	3.21 [c]	2.49	6.65 [c]	5.99	↘
DT2	64.32 [a]	17.95	97.55 [b]	30.55	46.60 [c]	11.52	38.42 [c]	23.17	↘
FMRev	4.24 [a]	0.98	3.21 [b]	0.58	5.29 [c]	1.16	4.33 [a,c]	2.06	↘
FDRev	43.69 [a]	17.13	40.86 [a]	37.14	138.61 [b]	44.08	106.49 [b]	42.09	↗
FXLow	1.10 [a]	0.54	1.02 [b]	2.40	6.94 [c]	5.71	3.87 [a,b,c]	6.21	↗
Rrisest	0.13 [a]	0.08	0.07 [b]	0.06	0.15 [a]	0.07	0.10 [a,b]	0.09	↗
Rfallst	0.05 [a]	0.03	0.04 [b]	0.06	0.14 [c]	0.06	0.10 [a,c]	0.09	↗

Reg: percentage of regulation (%); MMaxMst, MMinMst, and MT2st: magnitude of maximum monthly flow, minimum monthly flow, and 2-year recurrence flow (standardized to the mean annual flow; unitless), respectively; TMaxM and TMinM: timing of the maximum and minimum monthly flows, respectively (being 1 May and 12 April). TXLow and TT2: timing of the extreme low flows and of 2-year recurrence flow (Julian days); DMaxM and DMinM: duration of the maximum and minimum monthly flows, respectively (#months). DXLow and DT2: duration of extreme low flow conditions and of 2-year recurrence flow events (#days); FMRev, FDRev, and FXLow: frequency of the monthly flow reversals, daily flow reversals, and extreme low flows (# per year), respectively; Rrisest and Rfallst: daily rate of flow rise and fall, respectively (standardized to the mean annual flow; unitless). Further details on hydrological variables are available in Annex 1.

2.2. Data Analysis

Differences between flow regulation groups (i.e., free-flowing, low regulated, moderately regulated, and highly regulated) for each hydrological variable were tested with a Kruskal–Wallis test followed by a multiple comparison BH (Benjamini–Hochberg) test. This was appropriate because the data were not distributed normally. We used the R package "dplyr" [20] in R 3.6.1.

Three vegetation metrics were computed. First, we computed the 'species richness'(#) within the woody, graminoid, and forb functional groups for each regulation group as the number of species from each life form present in free-flowing, low-, moderately-, and highly-regulated reaches. Second, we computed the 'relative abundance' (%) of each life form for each regulation group (i.e., mix of plant life forms) as the ratio between the species richness within each life form (see above) and the total number of species (including woody species, graminoids and forbs) present at each regulation group. Third, we computed the 'relative presence'(%) of the species within each life form in each flow regulation group as the number of reaches from a regulation group where a species was present in relation to the total number of reaches of that regulation group.

Afterwards, we fitted linear regressions for each individual species with 'relative presence' as dependent and the 'percentage of regulation' as independent variables, and we extracted the regression coefficients using the lme4 package in R [21]. A positive regression coefficient indicates that the species benefits from regulation (i.e., the presence of the species is more likely when regulation intensifies), whereas a negative coefficient indicates that the species is disfavored by regulation (i.e., the presence of the species is less likely when regulation intensifies). From the pool of all species, we also noted whether each species from each life form were (i.e., appeared) or were not (i.e., disappeared) in reaches beyond 15% regulation (i.e., moderately and highly regulated). For the interpretation of the results, we clustered the individual species in the following response groups: positive response (i.e., species with regression coefficients >2), negative response (i.e., regression coefficient <−2), impassive response (i.e., regression coefficient <2 and >−2), present only when regulation is beyond moderate (>15%), present only when regulation is high (>60%), absent when regulation is beyond moderate (>15%), and absent when regulation is high (>60%). By 'regulation beyond moderate' we mean in moderately regulated reaches, in highly regulated reaches, or in both, whereas by 'high regulation,' we mean only in highly regulated reaches. Subsequently, we calculated the percentage of species in each response group for each life form group.

Finally, we ran three canonical correspondence analyses (CCA), explored to what extent the hydrological variables drive species assembly within each life form, and identified which hydrological variables play key roles. We used the presence–absence-species-by-reaches dataset and the hydrological data per reach as the input and tested the significance of the CCA models and axes using the R package "vegan" [22]. The relative importance of each hydrological variable was evaluated using the loadings on the first three axes that were extracted. Higher loadings indicate a higher importance of that variable for that axis and thus for the spread of species along that axis. We considered 0.45 as the threshold of significance [23]. For the interpretation of the results, we indicated species by their response groups to flow regulation. Statistical analyses that were performed in R used the 3.6.1 version [24].

3. Results

3.1. Hydrological Variables

All hydrological variables differed significantly ($p < 0.05$) among flow regulation groups except for the duration of the minimum monthly flows (Table 1). Multiple comparisons tests showed that differences between regulation groups reflected decreased long-time scale (i.e., intra-annual) flow variation but increased short-time scale (i.e., daily) flow variations. That is, when comparing groups with increasing levels of flow regulation, we observed an increased magnitude of the minimum monthly flows, an increased duration of the maximum monthly flows, an increased frequency of the daily reversals and extreme low flows, and increased rates of change in the daily discharge, as well

as delayed maximum monthly flows and two-year floods. Furthermore, we observed a decreased magnitude of the maximum monthly flows and two-year floods, a decreased duration of the extreme low flows and two-year floods, and a decreased frequency of monthly reversals and early minimum monthly and extreme low flows (Table 1). In summary, these changes indicated that regulation stabilizes intra-annual flows but results in highly fluctuating and faster daily flows, earlier minimum and later maximum flows, and shorter extreme high and low flow events

3.2. Riparian Plant Species and Life Forms

Across the 94 study reaches, 372 plant species consisting of 44 woody species, 107 graminoids, and 221 forbs were found. In each life form, species richness decreased across categories with increasing flow regulation (Figure 2a). When comparing free-flowing conditions to high flow regulation, species richness decreased, on average, by 20% for woody species, 40% for graminoids, and 45% for forbs (Figure 2a). While the decrease was rather gradual for woody species, there was a more sudden decrease in species richness between free-flowing and 'low regulation' for the graminoid and forb species (Figure 2a). The diversity of the forb species substantially contributed to the diversity in natural riparian zones, with the ratio of relative abundance between woody, graminoid, and forb species being 13/29/58 (Figure 2b). Due to a slight increase in relative abundance of woody species and a decrease in the relative abundance of herbaceous species (graminoids and forbs), the herbaceous:woody ratio decreased from 6.7 in the free flowing category to 4.4, 5.7, and 5.1 in the low, moderate, and high flow regulation categories, respectively (Figure 2b).

Across all functional groups, the relative presence of most species correlated negatively with the degree of flow regulation (Figures 3a and 4; Annexes 3 and 4). A relatively higher percentage of woody species had a strong negative correlation compared to graminoids and forbs, among which, many showed an impassive response. That is, negative responses were observed for 61%, 44%, and 36% of woody, graminoid, and forb species, respectively (Figure 3a). Additionally, the mean response within those groups differed, with the average regression coefficient being −8 (±6.6 standard deviation) for woody species, −6 (±6.1 SD) for graminoids, and −4 (±4.4 SD) for forbs. The relative presence of fewer species correlated positively with the degree of flow regulation, and the same fraction of species in each life form group showed a positive response to increased regulation (i.e., 11% woody species, 16% graminoids, and 13% forbs) (Figure 3a). The strength of the relationship did not differ much between life forms (on average +3.0 (±3.0 SD)). While almost half of the graminoid and forb species were impassive to regulation, only a quarter of the woody species were impassive (Figure 3a).

A high number of species was solely found in free-flowing reaches, irrespective of life form. Furthermore, 70% of all woody, 46% of all graminoid, and 53% of all forb species found in the entire study grew along reaches with a free-flowing and/or low-regulated flow regime. A lower fraction of species was sensitive to high regulation, as 9% of all woody, 20% of all graminoid, and 6% of all forb species were absent in reaches with highly regulated flow regime (Figure 3b and Annex 3). In contrast, only a few graminoid and forb species were restricted from free-flowing and/or low-regulated reaches, as 4% of all graminoid and 5% of all forb species only occurred in reaches with an above moderate flow regulation, with, respectively, 1% and 2% of the species occurring exclusively in reaches with high flow regulation regimes (Figure 3b and Annex 3). No woody species were restricted to reaches with a higher flow regimes.
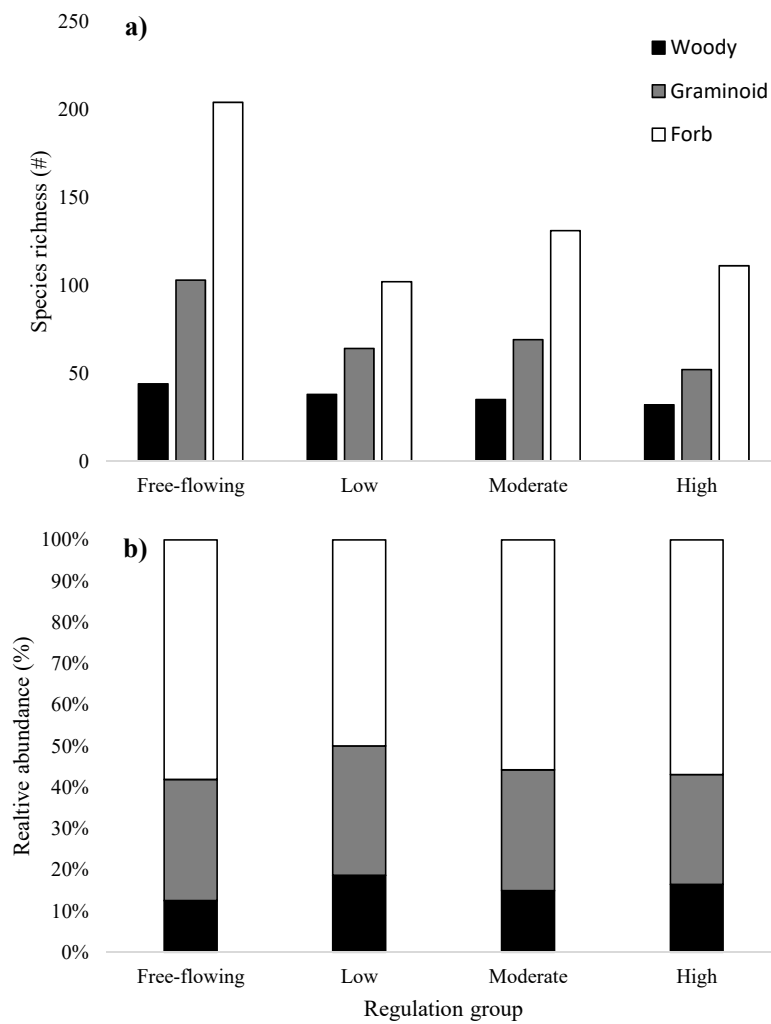
Figure 2. (**a**) Species richness within each life form group for each flow regulation group and (**b**) relative abundance of each life form group for each flow regulation group. Regulation groups involve the following levels of regulation: free-flowing (<0%), low (>0% and <15%), moderate (>15% and <60%), and high (>60%).
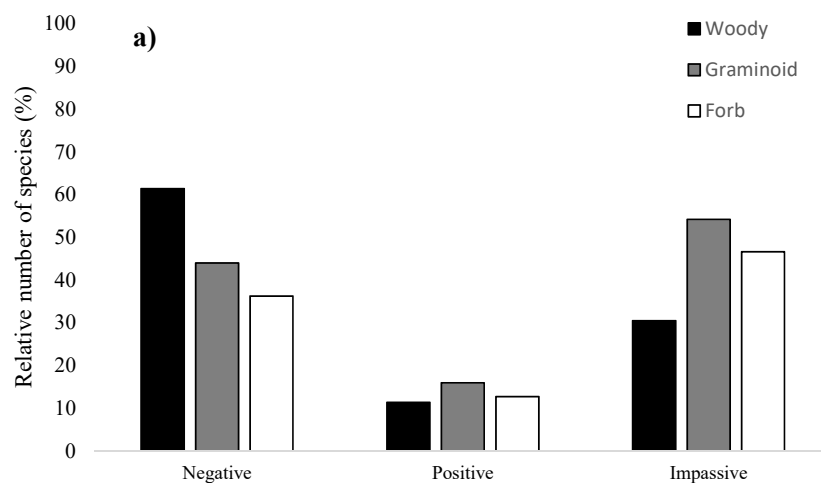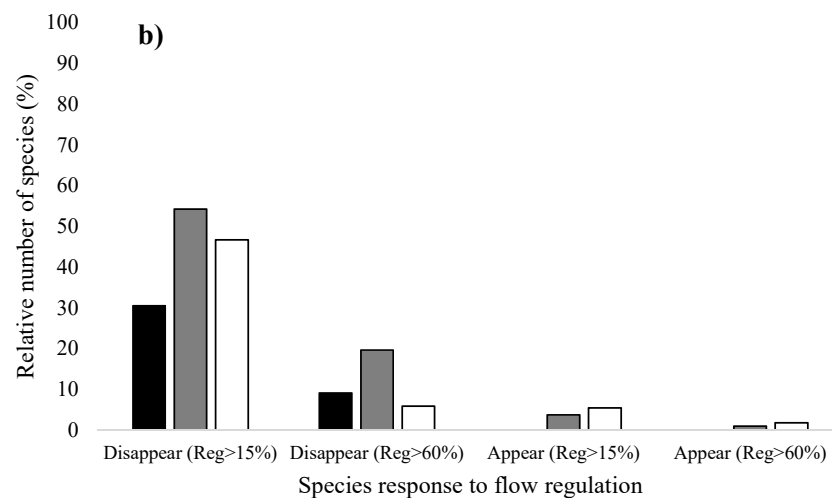

Figure 3. *Cont.*

Figure 3. Fraction of species separated by their response to flow regulation for each life form group. (**a**) Fraction of the total species pool which showed negative, positive, or impassive responses to increasing degrees of regulation. (**b**) A specification of the above showing the fraction of total species that disappeared or appeared at reaches with beyond moderate flow regulation (>15%) or in the high flow regulation category (>60%).

The three CCA models (i.e., for woody species, graminoids, and forbs) were statistically significant (Table 2). The first two CCA components were significant in each CCA model, whereas the third and fourth components were significant for the woody and forb species but not for the graminoid species (Table 2). The highest cumulative variance was observed in woody species, for which the selected hydrological variables explained up to 52% of the variance in the first three axes, whereas 49% and 40% variance was explained by the first three axes for graminoids and forbs, respectively (Table 2). Woody species showing positive, negative, and impassive trends in response to increased degrees of flow regulation were well segregated in CCA space. Negative trends were found for willow *Salix glauca* L., mosses (*Lycopodium selago* (L.) Bernh. ex Schrank & Mart. and *L., annotinum* L.), heaths (*Vaccinium microcarpum* Aiton, *Vaccinium oxycoccos* L., *Andromeda polifolia* L., and *Ledum palustre* L.), *Betula nana* L., *Linnaea borealis* L., and *Rosa majalis* Herrm., whereas most willows (*Salix herbacea* L., *Salix lapponum* L. and *Salix pentandra* L., *Salix lanata* L., *Salix triandra* L., *Salix hastata* L., *and Salix cinerea* L.) along with other shrubs such as the black and red currants (*Ribes ningrum* L. and *Ribes rubrum* L.), raspberry (*Rubus idaeus* L.), and trees such as birches *(Betula pendula* Roth *and Betula pubescens* Ehrh.) showed marked positive or impassive trends with regulation (Figures 4 and 5; Annex 5). Hydrological variables that were strongly correlated to woody species arrangement in CCA space were related to the percentage of regulation, extreme low flow conditions (duration, frequency, and timing), monthly flows (magnitude of maximum and minimum), and daily flows (frequency of reversals and fall rates) (Figure 5 and Table 2). In general, woody species with positive and impassive trends were separated along the second axis that aligned with a higher percentages of regulation and related hydrological characteristics such as shorter, more frequent, and earlier extreme low flow periods; lower maximum but higher minimum monthly flows; and more frequent and faster daily flow reversals. These latter two had highest loading on the second axis (Figure 5 and Table 2). The opposite was true for species characterized by negative trends.
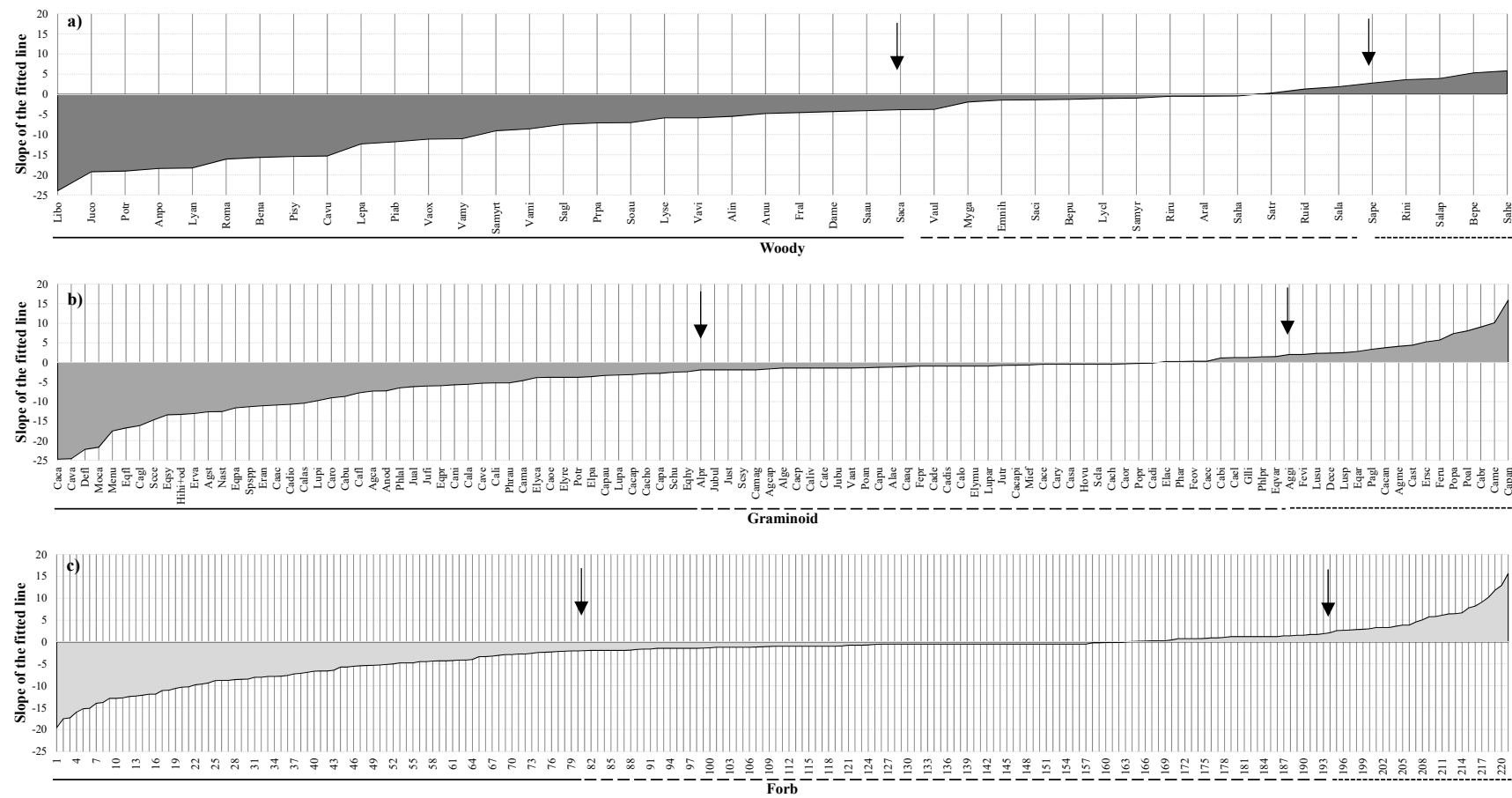
Figure 4. Regression coefficients of the species-specific linear regressions between the relative presence of a species and the mean percentage of regulation separated for each life form group (Woody species (**a**), graminoids (**b**) and forbs (**c**)). Different regression coefficients are indicated with a line below and with arrows at the top of each. The full names of the species are in Annex 1.

Table 2. Summary table of the variable loadings and cumulative variance explained of the first three axes of the CCA, separated for woody, graminoid, and forb species distribution data. In addition, the significance of each axes in each CCA is provided (bottom row), as is that of the CCA as a whole (top row). For an explanation of the hydrological variable names see Table 1 and Annex 1. We highlight the cells (bold) with loadings beyond 0.45.

	Woody Species (F = 2.08, p = 0.001)			Graminoids (F = 1.76, p = 0.001)			Forbs (F = 1.99, p = 0.001)		
	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3
Reg	0.29	**0.56**	0.17	**−0.46**	0.09	0.00	0.14	−0.08	**−0.47**
MMaxM_std	−0.07	**−0.46**	−0.11	0.22	−0.07	0.06	0.11	0.19	0.27
MMinM_std	−0.17	**0.55**	−0.03	−0.11	0.18	0.13	−0.17	0.04	−0.40
MT2_std	−0.08	−0.28	−0.10	0.28	0.04	0.14	−0.03	0.25	0.07
TMaxM	0.29	0.13	0.30	−0.37	0.01	−0.22	0.21	−0.06	−0.24
TMinM	−0.01	−0.22	0.03	0.04	−0.39	−0.05	0.22	−0.21	**0.53**
TXLow	−0.01	**−0.46**	0.29	0.04	−0.18	−0.20	0.10	−0.22	0.32
TT2	0.30	0.39	**0.50**	**−0.72**	0.26	−0.11	0.30	−0.22	**−0.56**
DMaxM	0.00	0.35	0.33	−0.14	−0.01	−0.25	−0.09	−0.07	−0.07
DMinM	−0.41	0.35	0.34	−0.04	0.11	−0.32	−0.29	−0.24	−0.04
DXLow	**−0.46**	−0.14	0.04	0.40	0.14	**−0.67**	**−0.54**	−0.29	0.41
DT2	0.10	−0.28	0.21	−0.27	−0.32	−0.32	0.20	−0.38	0.36
FMRev	−0.15	0.17	**−0.59**	0.31	0.13	**0.47**	−0.12	**0.64**	−0.05
FDRev	0.03	**0.63**	0.01	−0.21	0.30	0.27	−0.01	0.17	**−0.64**
FXLow	**0.43**	**0.66**	−0.15	**−0.45**	0.18	0.34	0.18	−0.09	**−0.53**
RRise_std	0.17	0.15	−0.13	0.02	0.17	0.33	0.08	0.26	−0.34
RFall_std	0.34	**0.60**	−0.04	−0.41	0.14	0.26	0.24	−0.07	−0.53
Eigenvalue	0.10	0.07	0.05	0.14	0.12	0.08	0.18	0.13	0.09
Proportion Explained	0.23	0.17	0.12	0.20	0.17	0.12	0.18	0.13	0.09
Significance of axis	p = 0.001	p = 0.001	p = 0.027	p = 0.049	p = 0.072	p = 0.113	p = 0.001	p = 0.001	p = 0.003
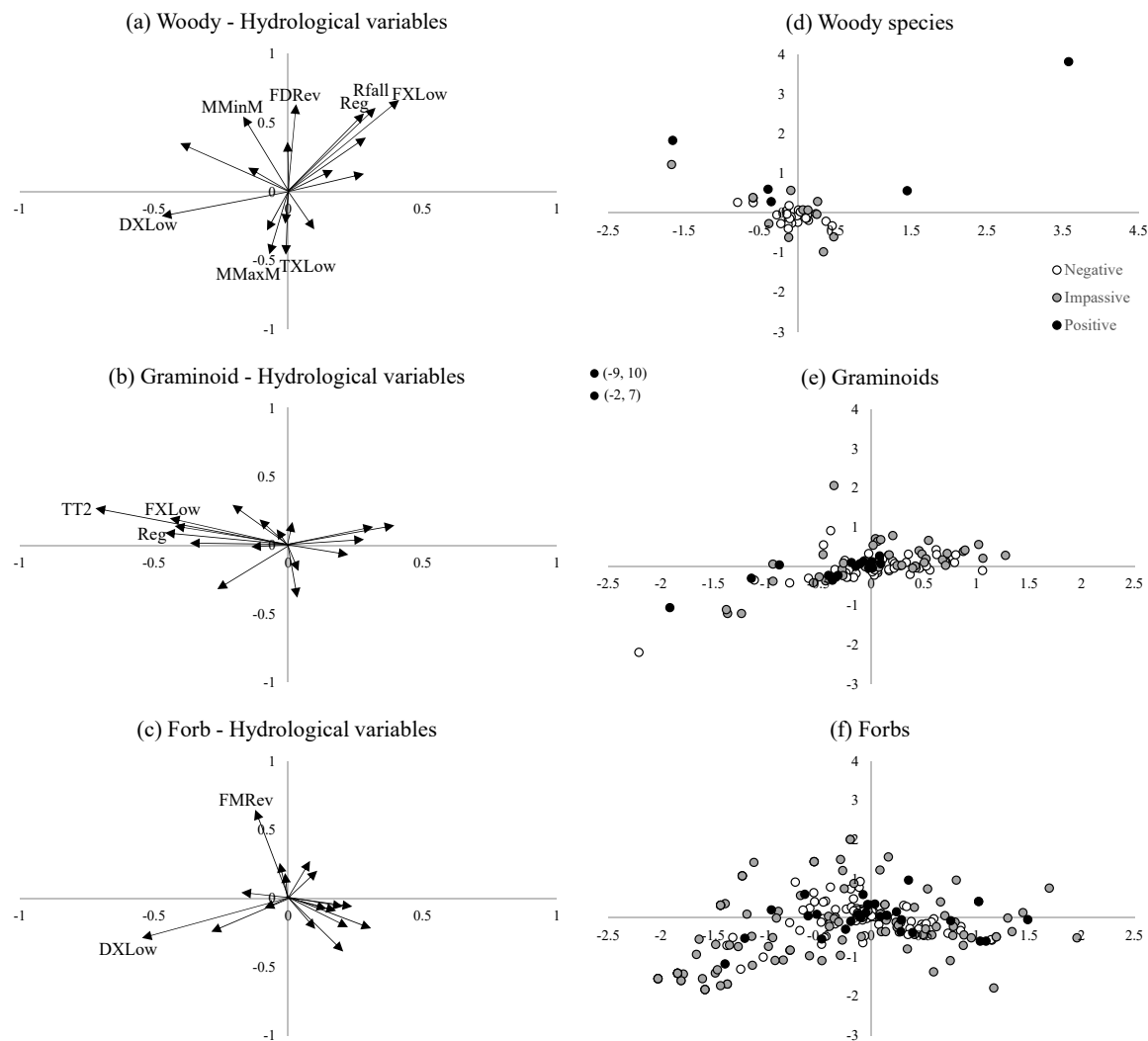
Figure 5. Biplots of the canonical correspondence analyses (CCA) on woody (**a**,**d**), graminoid (**b**,**e**), and forb (**c**,**f**) presence–absence species data. (**a**–**c**) represent the canonical loadings for the hydrological variables, and (**d**–**f**) show species scores. For a better visualization, only hydrological variables with loadings of >0.5 are labeled. Each point is one species, with the fill color representing species response to increased flow regulation being: negative (white dots), positive (black dots), and impassive (grey dots) trends. The two dots at the top left corner in (**e**) represent two species outside the range of the x- and y-axes; their coordinates are indicated between parentheses. An explanation of the codes of the hydrological variables are in Table 1 and Annex 1.

Graminoid species with different responses to flow regulation were not as well segregated in the CCA space as woody species. However, species with positive trends were located more to the left of the first axis (Figure 5). Among graminoids that showed negative trends to increased flow regulation, we found several *Carex* species (*Carex acuta* L., *Carex Lasiocarpa* Ehrh., *Carex rostrata* Stokes, and *Carex vesicaria* L.), as well as *Alopecurus aequalis* Sobol, *Eleocharis palustris* (L.) Roem. & Schult., *Phragmites australis* (Cav.) Trin. ex Steud., *Schoenoplectus lacustris* (L.) Palla, *Juncus bulbosus* L., and *Equisetum fluviatile* L. (Figures 4 and 5, Annex 5). Positive and impassive trends were frequently observed in the genus *Poa* sp., *Carex* sp, and *Festuca* sp. For instance, *Poa glauca* Vahl and *Poa alpina* L. showed strong positive trends, while *Poa annua* L. and *Poa pratensis* L. were impassive to regulation. Within *Carex* sp., positive responses were found for *Carex panacea* L., *Carex brunnescens*, (Pers.) Poir. and *Carex canescens* L., but many *Carex* species were impassive to regulation (e.g., *Carex elongata* L., *Carex bigelowii* Torr. ex Schwein., *Carex ornithopoda* Willd., *Carex capitata* L., *Carex saxatilis* L.,

Carex digitata L., *Carex livida* (Wahlenb.) Willd., and *Carex loliacea* L.). Species from the genus *Festuca sp.* (e.g., *Festuca vivipara* (L.) Sm., *Festuca rubra* L., and *Festuca ovina* L.) also responded positively to regulation. Other graminoids with positive trends to increased flow regulation were: *Eriophorum scheuchzeri* Hoppe, *Calamagrostis chalybaea* (Laest.) Fr. and *Calamagrostis stricta* (Timm.) Koeler, *Juncus trifidus L.*, *Alopecurus aequalis* Sobol., *Juncus trifidus* L., and *Agrostis mertensii* (Trin.) Kuntze (Figures 4 and 5; Annex 5). From the CCA, it became clear that a considerably smaller number of hydrological variables explained this arrangement for graminoids on the first two axes compared to woody species. Positive and impassive trends of graminoids aligned with higher percentages of regulation and, subsequently, more frequent extreme low flows and delayed floods (Figure 5). The opposite was true for species with negative trends to increased flow regulation.

Finally, forb species with positive, negative, and impassive trends in response to increased flow regulation were mixed in the CCA space (Figure 5). For example, *Sedum rosea* L., *Erigeron borealis* L., *Cerastium alpinum* L., *Persicaria foliosa* (H.Lindb.) Kitag. *Cicuta virosa* L., and *Arabis arenosa* L. showed positive trends, whereas *Euphrasia frígida* Pugsley, *Euphrasia stricta* Kunth, *Melampyrum pretense* L., *Persicaria lapathifolia* (L.) Delarbre, and *Spergula arvensis* L. showed negative trends (Figure 4), but all were scattered throughout the biplot (Figure 5 and Annex 5). A couple of hydrological variables correlated to forb species arrangement, with variation along the first axis being related to decreased intra-annual flow fluctuation (i.e., frequency of monthly reversals) and variation along the second axis being related to an increased duration of the extreme low flows (Figure 5 and Table 2). Unlike the CCA of the other life forms, the variable 'percentage of regulation' had a minimal effect on species distribution, as indicated by much lower axes loadings for this variable in the forb CCA compared to the CCA's of the other life forms (Table 2).

4. Discussion and Conclusions

The high spatial and temporal heterogeneity of environmental conditions such as hydrology, geomorphology, light, and temperature determine the richness and distribution of plants along riparian zones of free-flowing rivers. Hydrological factors, however, are seen as the most important ones [25]. In boreal streams, hydrological heterogeneity results from a flow pattern with a strong seasonality and ice disturbance. During fall and winter, flows are low, while during spring, large and snowmelt-driven floods shape rich riparian plant communities. Characteristic riparian forbs, graminoids, shrubs, and trees are arranged as clear belts at different elevations, parallel along the channel because each life form is thought to have a different resistance to the hydrological forces of the spring flood [26]. Naturally recurrent ice disturbance usually restrains the development of woody plants at lower elevations, while it favors annual and biennial species (i.e., mostly forbs) or perennial hemicryptophytes that die back to ground level during winter. The natural flow conditions imposed by the spring flood can explain the typically high ratio between herbaceous and woody species in the riparian areas of boreal free-flowing rivers [27].

In our study area, river regulation is mostly due to hydropower production, and the selected hydrological variables showed that it drastically alters flow regimes at long and short times scales. At long time scales, it evens out differences in monthly flows, induces shorter, more frequent, and earlier extreme low flows, and it also delays floods. At short time scales, regulation enhances daily flow fluctuations, with hydropeaking in some extreme cases [28]. Our results reinforce other studies demonstrating that flow alterations that are associated with regulation translate into declined riparian diversity and modified riparian community composition [29–31]. Our study showed how flow regulation through changes in various flow attributes exerts differing effects over specific riparian life forms and breaks the balance between them that exists in riparian communities along free flowing rivers.

The substantial decrease in the herbaceous:woody species ratio, as observed in regulated reaches in our study, suggests stronger impacts of regulation on the richness of graminoids and forbs compared to woody species. Unlike the authors of [32], who described the almost complete disappearance of shrubs and trees over the herbaceous species following dam-induced changes in the winter flooding

in the Yangtze River, in our study, the richness of herbaceous species (the sum of graminoids and forbs) declined more strongly with increased regulation compared to woody species (both in absolute numbers as well as a net reduction, i.e., the species that appear minus the ones that disappear). Herbs, characterized by short generation times and ruderal life strategies, seem to be especially affected by long-term flow stabilization, as such species benefit from natural formation of disturbance patches [33]. Such bare patches allow for germination, and other studies on the effect of river regulation on species diversity have frequently associated reduced species richness with difficulties in germination and establishment [32–35]. In addition to recruitment, those bare patches may change the competition among woody, graminoid, and forb species. In riparian systems, frequent occurrence of disturbances could relax competition for resources, especially light [12,36]. The observed shift towards less short-lived species in our regulated rivers is therefore consistent with life-history theories regarding adaptations to disturbance [33,37]. Empirical studies in riparian zones further confirm that annuals increase following increased flooding and/or give way to perennials with increased time since major flood disturbance [30,32,38–40]. A field experiment in riparian zones in the semiarid savanna showed a comparable recruitment of grasses and forbs in treatments with and without water addition and disturbance [12]. In our study however, graminoids were more responsive to regulation than forbs.

The results of our CCA suggested that graminoid community composition seems to be particularly affected by regulation through delayed floods and more extreme low flow events, whereas forb community composition was less clearly affected by most hydrological variables, as only intra-annual flow stabilization was able to explain some of the variance. This somewhat contrasts results by the authors of [41,42] who found that herbaceous species are very responsive to changes in flow regime. The variability in the woody, graminoid, and forb community compositions that was unexplained by hydrological variables suggests that other environmental variables may co-determine community composition. Our results point that such other variables gain importance in herbaceous communities. In addition to hydrology, the variables of land-use, nutrient availability, soil moisture, air temperature, and light availability have been shown to be particularly critical for riparian community composition [43–45]. In addition to intra-annual flow stabilization, the alteration of many other hydrological variables was found to determine the community composition of woody species in our study. The community composition of woody species appeared to be sensitive to both long term (intra-annual) and short-term fluctuations in flows. On the one hand, the desynchronization of a species' life story stages with intra-annual flow regime patterns may strongly affect woody species, which highly depend on recruitment from seeds rather than clonal dispersal—as is common among herbaceous species [46,47]. Seed dispersal and establishment are highly dependent on flood schedules, and other studies in the same area [16] have described important impacts of regulation on woody species as being linked to, among other phenological traits, their particular dispersal and germination periods. On the other extreme, very frequent and rapid variations of daily flows related to intense hydropower production schemes may hamper woody species germination and survival [48,49]. Such short-term changes in flows cause repeated wetting and, ultimately, nearly permanent moist or inundated soils. In general, woody, graminoid, and forb species have intrinsically different water requirements and tolerances during most life stages, with graminoids and forbs being better adapted to waterlogged environments than woody plants [50,51].

In addition the described negative effects of regulation, the fact that few species from all life forms increased their presence along regulated reaches and that some graminoids and forbs only occurred at higher levels of flow regulation, demonstrated that meager positive effects may be also expected following regulation. According to the deletion/addition/replacement theory (i.e., assembly rules by the authors of [52]), species-specific differences in the ability to tolerate hydrological alterations may underlay the observed wide range of species responses. Eventually, this results in a non-random sorting of species along hydrological gradients [2,53] and across reaches with different degrees of regulation. Numerous examples from scientific literature have shown that woody species (both native and non-native) frequently take advantage of the new hydrological conditions and invade regulated

reaches (e.g., [54,55]). Though we found positive responses to increased flow regulation among woody species, there were no woody species that uniquely occurred in reaches with some degree of regulation. This may indicate dispersal limitations [56] or that requirements for establishment were not met under regulated conditions. Conversely, although of a relatively small number, the fact that new graminoids and forbs appeared in regulated reaches suggested that there is a source of new species from the upstream and upland herbaceous flora that can find success under the new hydrological conditions. However, no exotic species were found among new species appearing only in regulated reaches, which, on the other hand, is not surprising at this high latitude [57].

Woody, graminoid, and forb species coexist in the riparian areas, and flow regulation may affect those life forms differently, thus leading to unbalances in community composition. Our results showed that riparian diversity in boreal rivers is driven by graminoid and forb life forms, as well as that regulation, due to a reduction of graminoid and forb diversity, results in overall poorer communities. This agrees with trends in other plant communities suffering from pressures such as heavy logging and overgrazing [9]. When population and community structure are altered, an array of ecosystem functions can be affected too, in particular when shifts in community structure includes (major) shifts in plant functional types [58,59]. For example, impoverished riparian woodlands may ultimately stimulate bank collapse through reduced rooting structures, decreased nitrogen assimilation, and changed stream hydrology, temperature, and primary production [60]. Similarly, the impoverishment of the herbaceous riparian community may affect erosion-related processes like trapping and the storing processes of suspended sediment, or provisions of habitat and refuge for biota. This impoverishment may also induce changes in phosphorous assimilation [61]. Since riparian community composition also affects macroinvertebrate and fish assemblages, changes in the ratio between herbaceous and woody species following flow regulation may have cascading effects. For instance, salmonid fishes could be particularly negatively affected by changes in herbaceous community composition [62]. Moreover, unbalances between life forms may also influence the success of the restoration of degraded systems [63]. In conclusion, the modification of certain flow attributes in flow regulation schemes, as well as the intensity of these modifications, result in shifts in the relative abundance of woody, graminoid, and forb life forms, as well as changes of the within-group species richness and community composition. Consequently, flow regulation may alter the characteristic herbaceous:woody species balance of riparian plant communities, ultimately impacting the functions and benefits derived from riparian zones.

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