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# Title: The number of phenology patterns, not species richness, affects the greening season length of freely assembled plant communities

Running title: Complementarity and greening season

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## Abstract

Questions: Plant greening phenology is a key response trait that drives numerous ecosystem functions such as carbon storage and flowering. Plant communities with a diversity of phenology responses could show a longer greening season due to a more complete occupation of the temporal window available for growth. However, it is unclear how species composition and richness affect the phenology of local plant communities.

Location: This study was conducted in wetland landscapes of the St. Lawrence River in the province of Quebec, Canada (46.07° N; -73.17° W).

Methods: We used close-range digital imagery to monitor the greening phenology and species richness of 20 herbaceous plant communities from 2013 to 2016. We quantified the number of greening phenology patterns observed each year within each plant community using singular value decomposition of close-range image time-series.

Results: The number of plant species within plant communities was independent of the number of phenology patterns, or the length of the greening season. However, the number of phenology patterns correlated positively to the greening season length in all four years of monitoring.

Conclusions: The relationship between the number of phenology patterns and the greening season length suggests a complementary use of the temporal window available for growth within plant communities. Species richness was a poor indicator of the diversity of phenology responses in wet meadow communities. The absence of a positive relationship between the number of plant species and the diversity of greening phenology patterns, or the length of the greening season, suggests that other descriptors of plant communities are of importance. Species richness is more often than not a weak predictor of the functioning of local plant communities in the wild.

Key words: singular value decomposition, plant phenology, wetlands, timelapse imagery, species richness, functional diversity, remote sensing, biodiversity-ecosystem function relationship

## Introduction

The role of biodiversity on the functioning of ecosystems is a cornerstone of the conservation narrative. In vegetation sciences, biodiversity experiments are conducted by manipulating the species richness of plant communities subjected to similar climatic and edaphic conditions. (e.g., Hector et al., 1999; Tilman et al. 2001; Weisser et al. 2017). The underlying hypothesis of biodiversity experiments is that facilitation and functional complementarity among species in response to environmental variations determine the functioning of a plant community (Isbell et al., 2018; Wagg et al., 2017).

Greening phenology is attracting increasing attention in biodiversity research (e.g., Barry et al., 2019; Kraft et al., 2014; Oehri et al., 2017; Wolkovich et al., 2014). A practical definition of greening phenology for seasonal plants is the timing of green-on and green-off dates, which together determine the greening season length. Plant phenology data are now widely available at multiple observation scales, ranging from satellite imagery products (Bórnez et al., 2020; Jin et al., 2019; Li et al., 2019) to close-range networks of ground cameras (Brown et al., 2016; Mariani et al., 2012; Rheault et al., 2020; Richardson, 2019). While the various monitoring approaches of greening phenology tend to corroborate when aggregated at a large spatial grain (Richardson et al., 2018; Watson et al., 2019; Zhang et al., 2018), it is still unclear how species composition and richness dive the phenology of local plant communities.

Plant species richness could affect the greening season length due to a greater likelihood of finding species with a longer greening season in species-rich communities, or with complementary use of resources, leading to a more complete filling of the temporal window available for growth (Lasky et al., 2016; Rathcke and Lacey, 1985; Rheault et al., 2015; Schofield et al., 2018). Two recent studies reported that greening season length increases with increasing habitat heterogeneity and species richness of vascular plants in 1 km$^2$ landscapes (Oehri et al., 2017; Oehri et al., 2020). Similarly, close-range monitoring of 118 wetland plant communities by Rheault et al. (2021), over four consecutive years, revealed strong temporal and spatial complementarity effects of species assemblages on the greening season length at the landscape scale. Yet, the latter study showed that plant species richness *per se* did not influence the greening season of local communities within landscapes (Rheault et al., 2021). Other studies conducted in unmanaged ecosystems also did not systematically find a relationship between species richness and plant phenology (Lemmens et al., 2008, Rheault et al., 2015, Rheault et al., 2021), suggesting that other biodiversity facets could also be at play.

The above studies and results propose that the complementarity of plant phenology patterns over space and time could be a key determinant of the greening season length of a community, which may or may not be associated with species richness *per se*. A phenology pattern in this context is the unique green-on and -off seasonal signature of plants experiencing the same environmental forcing (e.g., Rathcke and Lacey, 1985). In the present study, we monitored the greening season length of 20 wetland plant communities over four consecutive years to: i) quantify the number of greening phenology patterns within plant communities using time-lapse photography and ii) evaluate if the number of greening phenology patterns correlates positively to species richness, and which of the two better explain the greening season length. We hypothesized that species richness should correlate positively to the greening season length of a plant community by supporting a broader range of greening phenology patterns. We will test the above hypothesis at the observation level of natural plant communities using an innovative approach based on timelapse photography.

## Methods

### Study site

We used data from one ecosystem of the SAuVER network (réseau de Suivi Automatisé de la Végétation des Écosystèmes Riverains), which monitors the phenology and species richness of wetland plant communities using timelapse cameras (Rheault et al., 2021). The dataset covered four years of greening phenology (2013 to 2016) on 20 herbaceous plant communities in the area managed by the Société de Conservation, d'Interprétation et de Recherches de Berthier et ses Îles (Quebec, Canada; 46.07°N; 73.17° W, Figure 1). The area is located within the biosphere reserve of Lake Saint-Pierre.

The littoral of Lake Saint-Pierre is flooded from April until May each year, with strong inter-annual variations in both amplitude and duration. Mean annual temperatures for the 2013-2016 period were 5.9°C, 4.5°C, 4.3°C, 6.3°C and total annual precipitation was 919.4 mm, 899.7 mm, 599.2 and 612.3 respectively. We assessed edaphic conditions in August 2015 by aggregating four soil samples from each plant community. Mean (± 1 SD) soil pH was 5.48 (± 0.23), soil moisture was 39.42% (± 13.02) and water table depth was 52.69 cm (± 35.82) (supplementary information in Rheault et al., 2021).

All plant communities were located within an area of approximately 1 km2 (Figure 1). We selected communities that represent the gradient of plant species composition and richness observed within the area. We paired species-rich plant communities with nearby species-poor, dominated, plant communities to minimize the influence of local edaphic conditions on species richness (Rheault et al., 2021). The floristic composition was characteristic of wet meadow and high-marsh wetlands along the St.-Lawrence River.

Timelapse monitoring

We used timelapse cameras (Timelapse PRO, Wingscape, Alabaster, USA) to track changes in species richness and plant greening phenology (Rheault et al., 2021). At the margin of each plant community, we mounted a camera on a metal post at a height of 1.5 m. The camera pointed at the vegetation with an angle of approximately 45° below the horizon and photographed an area of approximately 16 $m^2$. We took three images per day (9h, 12h and 15h) and monitored plant communities from April until December of each year (2013 to 2016). All images were at a resolution of 1944 x 2592 pixels and stored in JPEG format.

## Species richness

We quantified species richness of each plant community through a visual assessment of four pictures taken on the 15th of June, July, August and September of each year. We used species richness of the sun-exposed vegetation layer, as it was more representative of the camera view field. We validated the taxonomic identity of the species observed within each image using exhaustive field surveys conducted once a year in each plot. The taxonomy follows VASCAN (Brouillet et al., 2022).  We previously demonstrated the effectiveness of this approach at capturing the species richness gradient of these plant communities (see Rheault et al., 2015).

## Community phenology

We monitored the greening phenology of all the vegetation located in 4 x 4 m plots using timelapse cameras. We used the protocol of the SAuVER network to determine the greening season length of each plant community each year (Rheault et al., 2021). Out of the 80 natural plant communities monitored (20 communities over four years), we could not use the information from 10 of those because of camera displacement or malfunctioning issues resulting in the loss of numerous pictures and difference in time-series length. First, we quantified the average green chromatic coordinate index ($G_{cc}$) of image pixels using the following equation:

$$Gcc = \frac{\mathrm{G}}{\mathrm{R+G+B}} \ , \qquad \text{Eq. 1}$$

where R, G and B represents the digital numbers in red, green and blue channels extracted using the raster package (Hijman,2020; Sonnentag et al., 2012). We resized each image to 194 x 259 cells by averaging the local $G_{cc}$ values using the 'aggregate' function in base R. Since the field of view of each camera was approximately 16 $m^2$, each resized cell represented an area of approximately 3 $cm^2$. We then averaged the $G_{cc}$ values across all cells within each image to monitor the greening season phenology of the whole plant community. We filtered Gcc time-series to reduce noise using the "medianFilter" function from the FBN package and rescaled values on the 0-1 interval (Andronache and Agnelli, 2012). We fitted a smoothing spline on each rescaled time-series using the "gam" function from the mgcv package to reveal the seasonal trend of $G_{cc}$ values (Wood, 2017). Green-up and green-down dates were found when rescaled $G_{cc}$ values increased above or decreased below a threshold value of 50% respectively (White et al., 1997). We defined the greening season length of each plant community as the number of days elapsed between green-up and green-down dates (for more details, see Rheault et al., 2021).

## Number of phenology patterns within plant communities

We defined a greening phenology pattern as cells of the plant community images that follow similar trajectories of Gcc values over the season. For example, if the greening phenology pattern of plants on the left of the image differs from those on the right (e.g., because they represent different species assemblages), then the community presents two phenology patterns. We note that cells of the image that are nonadjacent may share the same phenology pattern. We performed image processing and time-series analyses under the R programming environment (R Core Team, 2018).

Greening phenology patterns are "hidden factors" within the temporal dynamics of a plant community. Singular values decomposition (SVD) is a method of ordination that effectively finds such hidden factors in a high-dimensional space, where the number of singular values explaining a certain amount of the variation correlates positively with the number of distinct hidden factors (Ravi Kanth et al., 1998). In our study, the number of singular values is used as an index of the number of distinct greening phenology patterns in a community. The approach has been previously applied to timelapse photography and is described in details elsewhere (Proulx et al., 2009).

We performed the SVD analysis on the resized images of $G_{cc}$ greenness values stacked over the growing season. Thus, each community was represented by a spatial vector of 194 x 259 $G_{cc}$ values monitored over 154 days (June 15th to November 15th) and 462 pictures (three pictures per day) each year. We then extracted the singular values of each of these matrices of 462 rows by 50,246 columns (194 x 259 cells). We retained the number of singular values that explained 30% of spatio-temporal variance of Gcc values (Proulx et al., 2009).

In the context of our study, the SVD analysis asks the following question: How many greening patterns are present in an image time-series of $G_{cc}$ values? To answer this question, the percentage of explained variation must be fixed so that the number of greening patterns can vary among communities (Appendix S2). If the percentage is too small (e.g., < 20%), only a few singular values are retained and we lose discriminatory power. Conversely, if the percentage is too high (e.g., > 50%), noisy greening patterns are extracted instead of deterministic ones and, again, we lose discriminatory power (Proulx et al., 2009). Thus, we used the number of retained singular values at the 30% cutoff as an index of the number of greening phenology patterns observed on each time series The remaining 70% is considered as noise that can be attributed to vegetation movement, wind, sun position, shadow effects, and so on. Using cutoff values of 40% or 50% (i.e., considering 60% or 50% noise) did not qualitatively change the conclusion. We performed SVD analyses with the "svd" function in R (R Core Team, 2018).

We also assembled synthetic plant communities to demonstrate that any relationship between the number of phenology patterns and the greening season length is not an artifact of the SVD method. To do so, we used the $G_{cc}$ time series of the 20 plant communities monitored in 2015 as our pool of greening phenology patterns. We then simulated 100 $G_{cc}$ matrices of 194 x 259 cells and randomly assigned (with replacement) between 1 and 20 greening phenology patterns to these matrices using the "sample" function within R. We therefore created 100 synthetic plant communities consisting of a combination of unique greening phenology patterns varying between 1 and 20. We performed SVD analysis on each of the 100 synthetic communities using the same procedure described above for natural communities.

## Statistical analysis

We used synthetic communities as a benchmark to validate that the SVD analysis effectively captured the diversity of greening phenology patterns simulated, and that the number of extracted phenology patterns did not artificially correlate with the season length. We first inspected the relationship between the number of singular values extracted through SVD analysis and the number of simulated phenology patterns in synthetic communities. We also inspected the relationship between the number of singular values and the greening season length.

We then evaluated the independent contribution of plant species richness and diversity of phenology patterns (i.e., number of singular values) on the greening season length of natural communities. We inspected the following three bivariate relationships, with year as a random effect: i) species richness (explanatory variable) vs number of greening phenology patterns (response variable), ii) species richness (explanatory variable) vs greening season length (response variable), iii) number of greening phenology patterns (explanatory variable) vs greening season length (response variable). We assessed all the above relationships using linear regression models fitted with the "lmer" function from the lme4 package (Bates et al., 2015). For each model, we calculated the marginal and conditional $R^2$, representing the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively, using the R Package "performance" (Lüdecke et al., 2020).

## Results

Species richness varied from 2 to 11 species, and the greening season length from 81 to 148 days. We identified 46 plant species in total over the whole study period (see Appendix S1 in Supplementary information). The most dominant species was *Phalaris arundicaea* (reed canarygrass), which is an exotic invasive plant in this system. Other abundant species were *Calamagrostis canadensis* (bluejoint reedgrass, native*)*, *Onoclea sensibilis* (sensitive fern, exotic), *Lythrum salicaria* (purple loosestrife, exotic)*, Sagittaria latifolia* (broad-leaved arrowhead, native), *Sparganium eurycarpum (*broad-fruited burred, native*)* and *Eutrochium maculatum* (spotted Joe Pye weed, native), which characterize wet meadows. Rare species in this system included the native *Cuscuta gronovii*, *Cicuta bulbifera*, *Sium suave*, *Stellaria longifolia*, *Dulichium arundinaceum* and *Triadenum fraseri*, which are more representative of freshwater marshes (Appendix S3).

We simulated 100 synthetic plant communities randomly combining between 1 to 20 different phenology patterns. The greening season length of these communities varied from 100 to 145 days (Figure 2). We found a strong relationship between the number of singular values extracted through SVD analysis and the number of simulated phenology patterns (Figure 1a; $R^2 = 0.96$, slope = 4.39, $t = 51.44$, $p < 0.001$). The slope of the model indicates that SVD analysis underestimated the number of phenology patterns by a factor of four, although the correlation is overall strong. As expected, we did not find any relationship between the number of singular values and the greening season length (Figure 1b; $R^2 = 0.03$, slope = 0.88, $t = 0.73$, $p = 0.42$).

We did not find any relationship between plant species richness and the number of singular values (i.e., number of greening phenology patterns; Figure 3a; marginal $R^2 < 0.01$, overall slope = -0.08), or between plant species richness and greening season length (Figure 3b; marginal $R^2 = 0.04$, overall slope = -1.31). However, we did find a positive relationship between the greening season length and the number of greening phenology patterns within freely assembled plant communities of the SAuVER network (Figure 3c; marginal $R^2 = 0.21$, overall slope = 1.30). We observed the latter relationship in each of the four years (Figure 3c).

## Discussion

We showed that increasing the number of phenology patterns prolongs the greening season of wetland plant communities in the wild. We observed the relationship between the number of greening phenology patterns and season length in each of the four years of monitoring. In contrast, plant species richness did not affect the number of phenology patterns, nor the season length. These results support the prediction that plant communities with a higher number of phenology patterns show a longer greening season due to a more complete occupation of the temporal window available for growth. This temporal window also changes from one season to the next because of natural variability in environmental conditions, perhaps explaining the different slopes observed across years. However, species richness was not the driver of this temporal complementarity among phenology patterns within a plant community, suggesting that other coexistence processes are at work.

The number of greening phenology patterns in each plant community should mirror the functional response of species to both their biotic and abiotic contexts (e.g.: O'Connell et al., 2019; Dobbert et al., 2021). If species richness is the mechanism that lengthens the greening season of plant communities through temporal complementarity (e.g., Rheault et al., 2015), then richness should correlate to the number of phenology patterns. Alternatively, species richness may correlate to the greening season length of plant communities for reasons that are unrelated to temporal complementarity in phenology, such as the sampling effect; i.e., the probability of finding species with a long greening period increases with increasing species richness (Hector et al., 2002, Tilman et al., 1997). Neither of the above propositions were supported by our results, which rather point towards a species identity effect; i.e., the probability of finding species with the ability to tolerate a range of environmental conditions.

In a comprehensive synthesis of 119 experiments conducted on freely assembled plant communities, the results showed that, in 75% of cases, functional composition (i.e., species identity effect) was more important than biodiversity (i.e., species richness or related metrics) as a driver of ecosystem functioning (van der Plas, 2019). The same study also revealed that biodiversity - ecosystem functioning relationships, whether strong or not, are unaffected by functional composition, indicating that biodiversity and functional composition operate along different pathways (van der Plas, 2019). The above results are in line with those from the present study and support that plant biodiversity experiments conducted under controlled conditions may not be representative of naturally and freely assembled communities (e.g., Wardle et al., 2016).

Our findings suggest that intraspecific variation is a key driver of the functioning of plant communities. For example, the biomass production of individual plant species in assemblage vs monoculture communities (i.e., species relative yield) was shown to vary both ways by a factor 10 in forbs (Marquard et al., 2009) and a factor 3 in trees (Tobner et al., 2016). Species may either increase or decrease their relative yield, irrespective of species richness. Moreover, the seasonal dynamics of soil conditions within plant communities could shape the intraspecific variation of greening phenology patterns. In particular, soil water and nitrogen content are important determinants of the intraspecific variation of functional traits in wetlands (Born and Michalski, 2017, Moor et al., 2017). According to the leaf economic spectrum, plants with a higher specific leaf area and nitrogen content display a shorter leaf lifespan, which could influence their greening season length. Thus, plant communities with a higher functional diversity could host species with both long and short leaf lifespan, therefore increasing temporal complementarity among phenology patterns.

Over the four years of our study, reed canarygrass, bluejoint reedgrass and spotted Joe Pye weed dominated in a majority of communities with a longer greening season, irrespective of species richness. While long greening seasons were consistently associated with the above species, those associated with a short growing season were more idiosyncratic (Appendix S3, Supplementary information). In particular, communities dominated by the reed canarygrass could display the longest greening season in one year and the shortest season the next year (Rheault et al., 2015). The adaptation of reed canarygrass to a range of environmental conditions is well documented in the literature (Martina and von Ende, 2012). The species has naturalized from forage crop cultivars and display high levels of genotypic and phenotypic variability (Casler, 2010; Sahramaa, 2003).Plant phenology is a key descriptor of the functioning of ecosystems, which responds to changes in environmental conditions and drives processes such as carbon uptake and evapotranspiration (Morissette et al., 2009). Measures of plant phenology that are pattern-based, like in the present study, rather than species-based could be useful to assess the greening dynamics of plant communities. The SVD analysis of image time-series proposed here provides such a basis for assessing the greening season length and the number of phenology patterns within plant communities. Further work that disentangle the independent contribution of species and functional diversity on ecosystem functioning is critically needed.

## Conclusion

A strong negative relationship is often observed between the species richness of wetland communities and their ecological uniqueness, suggesting that communities dominated by a few plant species are often exceptional in terms of composition (Dubois et al., 2020). Furthermore, the positive influence of species richness on ecosystem functioning in freely assembled communities is often far less substantial than the relative effects of species composition and climatic factors (van der Plas, 2019). Studies focused on the greening season length as an ecosystem variable also reached similar conclusions (e.g., Oehri et al., 2017; Rheault et al., 2020). This was again obvious from the present study, where the greening season length of wetland communities was influenced by year-to-year change in environmental conditions, as well as intra-specific variation in the functional response of a few dominant species. Time may be ripe for the biodiversity-ecosystem functioning agenda to test other dimensions of biodiversity that are less species focused or dependent, especially in naturally assembled communities.

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## Author contributions

GR, RP and EL contributed to conceive and design the study. GR conducted the experiment and collected the data. GR, RP and YR analysed the data. GR lead the writing of the manuscript. GR, RP and EL contributed to the writing of the manuscript and gave final approval for publication.

## Data availability statement

The data are available in Appendix S4 of the supplementary information file.

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Figures

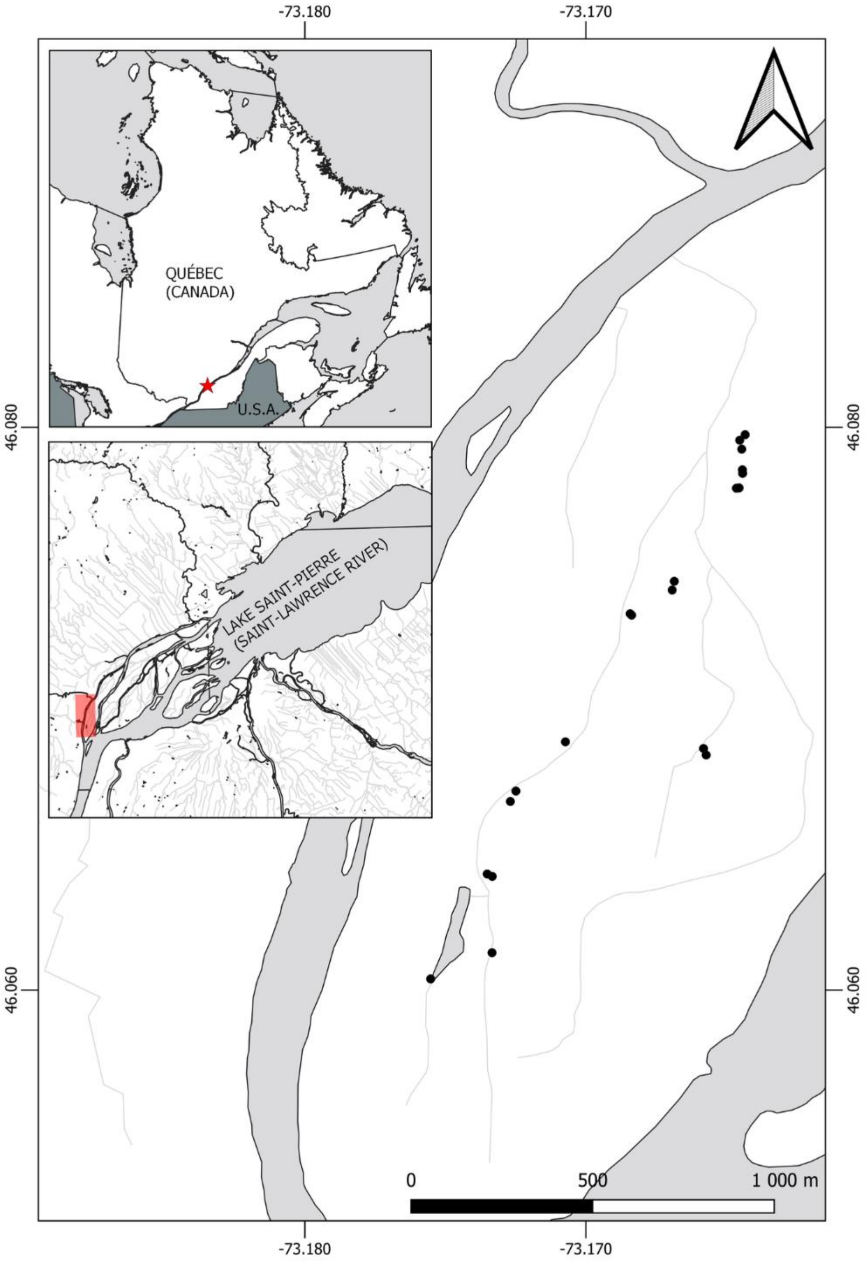

Figure 1. Location of the study area (insets) and of the 20 wetland plant communities used to monitor species richness and greening phenology in the Province of Québec, Canada.

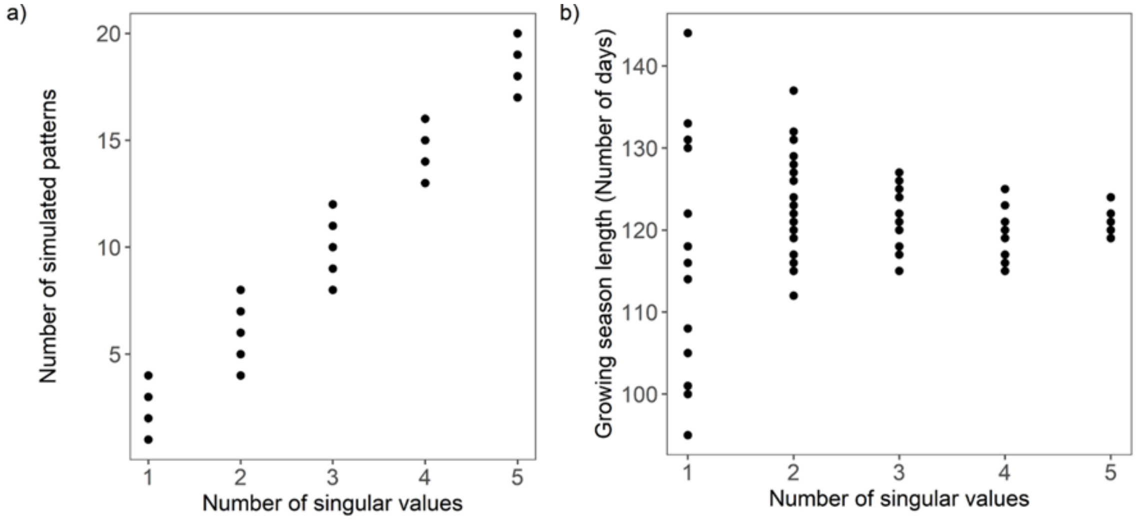

Figure 2. Correlations between the number of greening phenology patterns detected (number of singular values) and simulations of a) the number of phenology patterns, b) the greening season length. The numbers of singular values was extracted from the SVD of 100 simulated image time-series randomly combining 1 to 20 phenology patterns elapsing from 100 to 145 greening days.

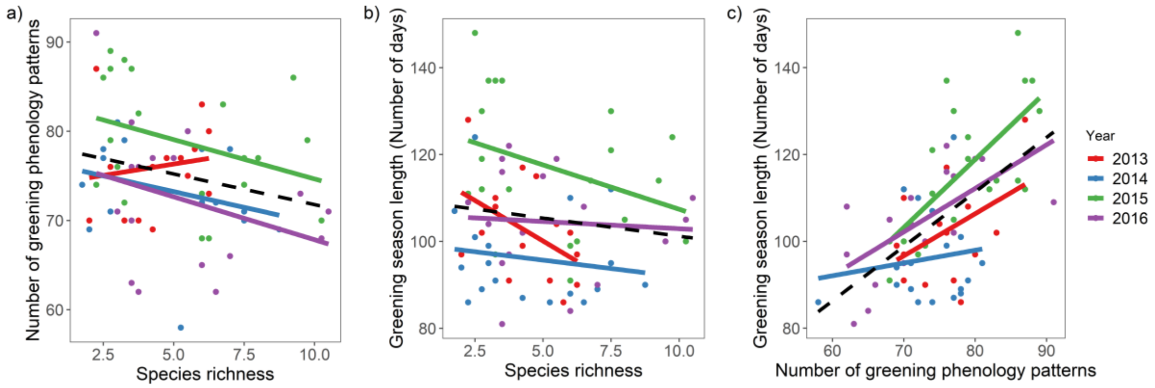

Figure 3. Analysis of 20 freely assembled wetland plant communities of the SAuVER network in the period 2013-2016. Linear relationships between a) number of greening phenology patterns and species richness, b) greening season length and species richness and c) greening season length and number of greening phenology patterns. Each color represents a different year and the dashed line represents the global relationship across all years. The number of greening phenology patterns is the number of singular values extracted from the SVD analysis of image time-series.

## Supporting information

Appendix S1. Rank abundance of the plant species observed across the 20 monitored wetland communities.

Appendix S2. Sensitivity of the SVD analysis to discriminate the number of greening phenology patterns in the image time-series.

Appendix S3. Identity of the dominant plant species associated to short and long greening seasons in 2013-2016.

Appendix S4. Dataset of species richness, number of greening phenology patterns and plant phenology values for 20 wetland communities in each of the four years of monitoring.