

Diversity of plant assemblages dampens the variability of the growing season phenology in wetland landscapes

Guillaume Rheault (✉ guillaume.rheault@uqtr.ca)

Universite du Quebec a Trois-Rivieres <https://orcid.org/0000-0003-4058-1893>

Esther Lévesque

Universite du Quebec a Trois-Rivieres

Raphaël Proulx

Universite du Quebec a Trois-Rivieres

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Abstract

Background: The functioning of ecosystems is highly variable through space and time. Climatic and edaphic factors are forcing ecological communities to converge, whereas the diversity of plant assemblages dampens these effects by allowing communities' dynamics to diverge. This study evaluated whether the growing season phenology of wetland plant communities within landscapes is determined by the climatic/edaphic factors of contrasted regions, by the species richness of plant communities, or by the diversity of plant assemblages. From 2013 to 2016, we monitored the phenology and floristic composition of 118 wetland plant communities across five landscapes distributed along a gradient of edaphic and climatic conditions in the Province of Québec, Canada.

Results: The growing season phenology of wetlands was driven by differences among plant assemblage within landscapes, and not by the species richness of each individual community (<1% of the explained variation). Variation in the growing season length of wetlands reflected the destabilizing effect of climatic and edaphic factors on green-up dates, which is opposed to the dampening effect of plant assemblage diversity on green-down dates.

Conclusions: The latter dampening effect may be particularly important in the context of increasing anthropogenic activities, which are predicted to impair the ability of wetlands to adapt to fluctuating environmental conditions. Our findings suggest that stakeholders should not necessarily consider local monospecific plant communities of lower conservation value to the global functioning of wetland ecosystems.

Background

Spatial and temporal variability of ecosystems has received a lot of attention in the last decades in the context of biodiversity loss, climate change and their impact on ecosystem functioning. Ecosystem functioning is known to vary i) among ecosystems due to the environmental context of each ecosystem, especially edaphic and climatic conditions [27]; ii) within ecosystems because individual communities respond differently to local conditions at the ecosystem scale [4, 42, 46, 50]; iii) inter-annually due to temporal variation in edaphic and climatic conditions [27, 50]; and iv) within communities because individual species respond differently to local conditions at the community scale [8, 17, 21, 26, 55]. In temperate and arctic regions, factors such as climate constrain the onset and offset of ecosystem processes [27]. During the growing season, competition for resources induces species specific responses to environmental conditions which have been hypothesized to be driving the observed variation among communities within the ecosystems and dampening the effect of edaphic and climatic conditions [46, 52]. The relative importance of these different sources of variation on ecosystem functioning has yet to be quantified in natural ecosystems and the dampening effect of the diversity of plant assemblages remains to be investigated.

Plant phenology is a key functional trait of plant that links growth and reproduction events of plants to the functioning of ecosystems [27]. Over large geographic extents, plant phenology is driven by the effect of climatic and edaphic factors on plant growth and stress tolerance [6, 18, 22]. In turn, plant phenology determines several ecological functions, such as pollination [14], herbivory [34] and carbon uptake [33]. One main advantage of studying plant phenology is that the timing of biological events can be monitored at high spatial and temporal resolution through satellite or time-lapse imagery [10, 54].

Although climatic and edaphic factors were identified as important drivers of plant phenology at both large and small observational scales, recent studies also emphasized the importance of species richness and composition [9, 28, 32]. Species subjected to similar climatic and edaphic conditions tend to show large interspecific differences in their phenology [11, 25, 49, 51, 54]. For example, Wilsey et al. [51] compared grassland communities in northern latitudes and found that their growing season length differed by nearly 40 days. A study by Meng et al. [25] reported large inter-annual variations in the flowering sequence (i.e., ranking order) of 15 co-occurring plant species. Thus, the biodiversity of plant assemblages could be an important driver of plant phenology by introducing spatial variability and temporal asynchrony within ecosystems.

Land managers and conservation biologists use estimates of plant species richness to characterize temporal changes in the ecological dynamics of ecosystems. Yet, the role of plant species richness on the regulation of plant phenology was investigated in a few cases only. A lengthening of the growing season with increasing plant species richness was observed across six biogeographic regions of central Europe, independently of altitude and land-use descriptors [28]. Rheault et al. [32] monitored 28 wetland plant communities and showed that the growing season length was, on average, 30 days longer in species-rich communities. However, the latter authors noted that the relationship between plant species richness and growing season length was contingent on the climatic conditions [32]. Studies of plant phenology have yet to disentangle the relative importance of species richness, community asynchrony, and community temporal variance on the dynamics of ecosystems.

The coefficient of variation of an ecological function (e.g., aerial biomass, growing season length) measured on several occasions is a standard measure of temporal variation; i.e., the reciprocal of stability. Using this metric, it can be shown that three key variables determine the temporal variability of a plant community [39]: i) species asynchrony, ii) species temporal variance and iii) species average functioning. Species asynchrony is a measure of how temporally de-correlated the functioning of each species is relative to the others in the community. The variability of a plant community will be low (i.e., stability will be high) if species asynchrony is high and if species temporal variance is low [39]. The above principles can be scaled-up to the ecosystem level, such that the variability of an ecosystem is this time determined by: i) community asynchrony, ii) community temporal variance and iii) community average functioning. For the diversity of plant assemblages to stabilize the functioning of ecosystems, the expectation is that community asynchrony is an important determinant, while community temporal variance is comparatively less important. High spatial variability in the average functioning of communities is also stabilizing because it buffers differences among ecosystems.

The objective of this study was to evaluate whether the growing season phenology of plant communities within wetland ecosystems is mostly determined by climatic and edaphic factors (i.e., ecosystem identity), by the diversity of species within plant communities, or by the diversity of plant assemblages. The approach that we developed in this paper consists of partitioning the growing season phenology of plant communities (green-up and green-down dates, and growing season length) into five components using linear models: i) Ecosystem identity, ii) Community temporal variance, iii) Community average functioning, iv) Species richness and v) Community asynchrony. A schematic representation of the partitioning procedure for growing season length is illustrated in Fig. 1. Disentangling between these alternative scenarios is critical because they involve different management scales and policies. We also provide a direct test of the diversity-stability relationship using the species richness of individual communities as a measure of plant diversity and the coefficient of variation of plant phenology (e.g., green-up date) as a standard measure of temporal variation.

Results

We successfully established a long-term monitoring network of plant phenology across five wetland ecosystems, which differed in their climatic and edaphic characteristics. Mean annual temperature in each ecosystem ranged from -4.6 °C to 6.4 °C, mean total annual precipitation from 661 mm to 1085 mm, soil pH from 3.5 to 6.4 and soil moisture from 40% to nearly 80% (Table 1). Mean green-up dates varied by almost a month among ecosystems, but mean green-down dates varied by no more than 12 days. The growing season length was on average 33 days longer at lower latitudes (Table 1).

Table 1
Environmental context of the five wetland ecosystems.

	Scirbi	Maskinongé	Lac-à-la-tortue	Bog-à-lanières	Umiujaq
Type	Wet meadows	Fluvial marshes	Peatlands	Peatlands	Wet meadows
Latitude	46.07	46.19	46.55	47.59	56.57
Nbr. Comm.	20	30	20	20	28
Temperature	6.40	5.10	4.80	2.00	-4.60
Precipitation	997.2	1009.3	1085.0	1016.4	660.8
Soil pH	5.48 ± 0.26	6.36 ± 0.28	3.47 ± 0.11	4.01 ± 0.11	5.38 ± 0.38
Soil moisture	39 ± 14	55 ± 15	78 ± 11	60 ± 13	58 ± 20
Green-up	160 ± 15	164 ± 8	147 ± 9	157 ± 7	172 ± 7
Green-down	266 ± 11	270 ± 15	263 ± 11	256 ± 8	258 ± 6
GSL	106 ± 15	112 ± 15	117 ± 12	99 ± 11	84 ± 10
<p>Wetland type (Type), latitudinal location (Latitude; Decimal Degrees), number of surveyed plant communities (Nbr. Comm.), mean annual temperature (Temperature; °C), mean total annual precipitation (Precipitation; mm), soil pH (Soil pH; Mean ± Sd), soil moisture (Soil moisture; %, Mean ± Sd), green-up date (Green-up, day of year, Mean ± Sd), green-down date (Green-down, day of year, Mean ± Sd), growing season length (GSL; number of days elapsed between Green-up and Green-down dates, Mean ± Sd). Mean and Sd values for soil pH and soil moisture were calculated from four measures in each plant community. Mean and Sd values for green-up, green-down dates and growing season length were calculated from all communities within each ecosystem over the period 2013–2016.</p>					

Using a hierarchical partitioning approach, we determined that Ecosystems identity was the most influential component for green-up dates, emphasizing the influence of climatic and edaphic factors on leaf-out events (Table 2). Community temporal variance (year identity within ecosystems) was the second most influential component for green-up dates. However, its influence diminished during the season, explaining no more than 15% of the variation in green-down dates. Community average functioning and Community asynchrony within ecosystems explained the largest share of variation in green-down dates. Species richness explained virtually no variation in the phenology of plant communities, whereas Community asynchrony explained more than 17% of green-up and green-down dates, highlighting the important role of compensatory dynamics in stabilizing the functioning of ecosystems (Table 2).

Table 2
Hierarchical partitioning of the variation in plant phenology.

Phenophases	Ecosystem identity	Community temporal variance	Species richness	Community average functioning	Community asynchrony
G-U	0.42	0.27	< 0.01	0.09	0.22
G-D	0.16	0.15	< 0.01	0.34	0.35
GSL	0.46	0.08	< 0.01	0.29	0.17
<p>Growing season phenology variation was explained by: Ecosystem identity, Species richness, Community temporal variance (year within ecosystem), Community average functioning (community identity within ecosystem), and Community asynchrony (interaction year x community identity). The values show the coefficient of determination (R^2) associated with each component when modelling the green-up date (G-U), the green-down date (G-D) and the growing season length (GSL).</p>					

Climatic and edaphic factors, represented by the combined effects of Ecosystem identity and Community temporal variance, contributed to more than two thirds (69%) of the variation in green-up dates. The result was reversed when considering the diversity of plant assemblages within ecosystems, represented by Community average functioning and Community asynchrony, which together explained 69% of the variation in green-down dates. The growing season length of wetland ecosystems reflected a balance between the destabilizing effects of climatic/edaphic factors on green-up dates and the stabilizing effects of the diversity of plant assemblages on green-down dates (Fig. 2).

Hierarchical partitioning of the variation unveiled the weak contribution of plant species richness in explaining the growing season phenology of plant communities. Among all possible combinations of years and ecosystems, we did not find any consistent relationships between plant species richness and growing season phenology (Table 2). Moreover, we did not find any evidence of a relationship between the average Species richness of a plant community and the inter-annual temporal instability of Green-up or Green down dates (Fig. 3, lower panels). To summarize, neither the phenology nor the inter-annual stability of a plant community was determined by its species richness (Fig. 3).

Discussion

The growing season length of wetlands reflected a balance between the destabilizing effects of climatic and edaphic factors on green-up dates and the stabilizing effects of the diversity of plant assemblages on green-down dates. Climatic and edaphic factors, expressed through Ecosystem identity and Community temporal variance, explained a larger relative proportion of the variation in green-up dates across ecosystems and years. Conversely, the diversity of plant assemblages, expressed through Community average functioning and Community asynchrony, explained a larger relative proportion of the variation in green-down dates, thus revealing a seasonal shift in the factors that drive the phenology of wetland ecosystems. Climatic and edaphic factors are destabilizing because they force plant

communities in a given ecosystem, in a given year, to converge towards a similar phenology. In this context, the diversity of plant assemblages is stabilizing because it allows plant communities to diverge into a portfolio of growth phenology patterns over space and time.

The destabilizing effect of climatic and edaphic factors on green-up dates may be attributed to the large latitudinal gradient covered by the SAuVER monitoring network. In high-latitude ecosystems, growth initiation is determined by climatic factors that control the activation of plant metabolism. [6, 24, 37]. In the specific case of wetland ecosystems, snowmelt and flooding events further determine the light available at the ground level and temperature profiles, as well as O₂ availability to plants [19, 44]. Given that spring temperatures, snowmelt dates, flooding amplitude and duration not only vary over space, but also from year to year, factors such as species composition and richness only have a weak dampening effect on green-up dates in comparison to climatic and edaphic factors.

Our findings, however, showed that the growing season length of ecosystems may be dampened by maintaining a diversity of plant assemblages in space and time. Previous studies have underlined the broad range of variation in the green-down dates of plant communities within ecosystems [9, 32]. Such variations in plant phenology reflect community-specific responses and adaptations to a similar set of climatic and edaphic conditions. Said otherwise, the broad range of green-down dates observed within a given region is largely driven by the ecology of plant communities. However, our data did not disentangle community-specific from species-specific responses to climatic and edaphic factors. A critical question in this context is whether the green-down phenology of plant communities is driven by a few keystones but functionally redundant plant species in the ecosystem [45]. A better understanding of the phenological strategy of each individual species will be required to tackle this question in greater depth.

Community asynchrony consistently explained 30 to 40% of the variation in the growing season length of plant communities, revealing the key role of compensatory dynamics in stabilizing wetland ecosystems. The early green-down of some plant assemblages in a given year was offset by the late green-down of other plant assemblages, and vice versa in other years. While species asynchrony was identified as a key principle for dampening the functioning of local patches of vegetation over time [e.g., 21, 55], our results suggest that community asynchrony may be just as important for dampening the functioning of ecosystems. Our findings did not support the hypothesis that local species richness stabilizes the functioning of plant communities, which contrasts with the results commonly reported from other biodiversity experiments [e.g.: 15, 30]. Among all possible combinations of years and ecosystems, we did not find a consistent relationship between plant species richness and plant phenology. Neither did we find evidences of a stabilizing effect of plant species richness on inter-annual fluctuations (temporal CV) in the growing season length of plant communities.

There is a growing body of literature emphasizing the importance of conserving a diversity of plant assemblages and not only high levels of local plant species richness. Dampening of ecosystem functioning through community asynchrony was so far only hypothesized by theoretical models and revealed in experimental grasslands [7, 16, 46, 50]. The present study is the first to report and replicate

this dampening principle on a large network of freely assembled plant communities spanning several ecosystem types. We showed that the community asynchrony principle operates independently of the climate and edaphic factors that prolong, or constrain, the growing season of plant communities. For instance, the growing season of plants in temperate and boreal ecosystems is predicted to last longer under a warming climate [e.g.: 3, 20]. Maintaining a diversity of plant assemblages may offer this insurance mechanism (aka portfolio effect; [42]) to the functioning of ecosystems in the face of rapid environmental changes.

Using the hierarchical partitioning framework developed here, we can provide another compelling example of the role of community asynchrony in dampening ecosystems. The Jena Experiment was specifically designed to study the effect of plant species richness on the functioning of managed grassland ecosystems, independent of species composition and other environmental drivers [35]. The dampening effect of plant species richness on the aboveground biomass production of these experimental grassland communities has been reported in several publications to date [e.g., 30, 36]. We retrieved publicly available aboveground biomass data covering 8 years and 82 grassland communities from the Jena Experiment [47] and fitted the model in Eq. 2 using aboveground biomass instead of growing season length as the dependent variable. To compare with the results obtained in the present study for the growing season length, we assigned 46% of the variation to Ecosystem identity (see Table 2) and focused on the remaining 54% of variation explained by Community temporal variance, Species richness, Community average functioning and Community asynchrony. The latter step was necessary because, in contrary to the SAuVER network, there is no variation between “ecosystems” in the Jena Experiment. Our reanalysis of the Jena experiment data showed that Community temporal variance explained 13%, Species richness 8%, Community average functioning 10% and Community asynchrony 22% of the spatial and temporal variation in aboveground biomass. Asynchrony in plant communities determined 22% of the variation in aboveground biomass in this system, compared to 8% for the species richness of plant communities. This analysis shows that the diversity of plant assemblages over space (Community average functioning) and time (Community asynchrony) have a potentially strong dampening effect on the above ground biomass production of experimental grasslands.

Conclusions

We revealed that dampening of temporal variation in the growing season of wetlands comes from the diversity of plant assemblages and their asynchronous responses, and not from maximizing the species richness of each individual community. While comparable in duration to other diversity-stability studies [e.g., 12, 13, 29, 41], we acknowledge that the observed variation in plant phenology is limited to only four years of data. Yet, the strength of the SAuVER network comes from the monitoring of many contrasted ecosystems using standard protocols. Years 2013–2016 were also not exceptional in terms of climatic conditions in the Quebec Province, so we are confident that our results will generalize on the long term. Dampening the functioning of ecosystems by maintaining a diversity of plant assemblages may be key in the context of increasing anthropogenic activities, which are predicted to impair the ability of wetlands to adapt to fluctuating environmental conditions [2, 23]. Hence, the diversity of plant assemblages should

be considered a conservation priority over local species richness, as it was shown to strongly dampen the functioning of ecosystems over both space and time. On the basis of these results, stakeholders should not necessarily consider monospecific plant communities as of lower conservation value to the global functioning of ecosystems. This is particularly true of wetland ecosystems, where local patches of vegetation tend to be naturally dominated by a few species. A reconsideration of conservation strategies is warranted to prioritize the conservation of natural wetland dynamics and the environmental heterogeneity that promote a diversification of plant assemblages within landscapes.

Methods

Experimental design

Wetlands represent an ideal system for studying the dampening effect of plant diversity on ecosystem functioning, as these ecosystems show large inter-annual variations in their growing season phenology and a high species turnover in space and time [32]. In 2013, we established a long-term monitoring network, called SAuVER, to monitor the taxonomic assemblage and growing season length of 118 plant communities across five wetland ecosystems (e.g.: arctic wet meadows, two peatland ecosystems, fluvial marshes and temperate wet meadows). Plant communities were monitored from 2013 to 2016 in the five ecosystems spatially distributed between 46°N and 56°N in Quebec (Canada; See Supplementary Fig. 1, Additional File 1). To minimize the effect of environmental heterogeneity on the phenology of plant communities in each ecosystem, we selected, within an area of less than one square kilometer, 20–30 plant communities mostly composed of herbaceous and low-shrub vegetation (See Supplementary Table 1, Additional File 1). We locally paired plant communities dominated by one or two species with nearby species-rich communities to create a species richness gradient that was independent of local environmental conditions (See Supplementary Fig. 2 and Supplementary Table 2, Additional file 1). Thus, differences among communities within ecosystems mostly reflect differences in their plant assemblages. By design, the SAuVER network emphasizes a gradient in species richness and the diversity of plant assemblages within in each ecosystem, thus maximizing beta diversity.

We used Wingscape timelapse cameras (Wingscape®, Albaster, USA) to monitor changes to the species assemblages (richness and identity), and the growing season phenology of plant communities. We programmed each camera to take three pictures per day (9 am, 12 pm and 3 pm), from April to December at lower latitudes, and from June to October at higher latitudes. The size of each image was 2592 × 1944 pixels and images were stored in JPEG format (RGB images). We left the cameras in the field the whole season, except in the fluvial marsh ecosystem where we took pictures on a weekly basis to prevent poaching. In the latter ecosystem, we mounted the camera on a metal post and followed the same procedure used in the other ecosystems. We positioned the cameras at a height of 1.3 m in peatlands and Arctic wet meadows, and 1.5 m in fluvial marshes and temperate wet meadows. Each camera was pointing downward towards the vegetation with an angle of 45 degrees, capturing a ground area of approximately 16 m² [32].

Field measurements

We conducted image-based taxonomic surveys of the overstory vegetation in each community through a visual assessment of four pictures taken on the 15th day of each month in June, July, August and September. We built a presence-absence community matrix and counted the total number of species present in the overstory of each plant community each year. To guide the identification process, we referred to an exhaustive botanical survey conducted in each ecosystem on a yearly basis. A pilot study of temperate wet meadows showed that the image-based taxonomic identification of plant species richness was highly correlated to field surveys [32]. Species richness of each community, each year, was determined as the mean number of observed species in the four samples. We used this variable in the variance partitioning procedure described below.

Plant phenology

We assessed the growing season length of plant communities using an automatic R procedure [31, 43]. In each image, we calculated a green chromatic coordinate index (G_{CC}) using the following equation:

$$G_{cc} = \frac{G}{R+G+B} \quad \text{Equation 1}$$

where R, G and B represented average red, green and blue pixels' digital numbers of each image [38]. We created G_{cc} time series for each community and year by assigning the median (50th percentile) of all available G_{cc} values within a non-overlapping moving window using the `medianFilter` function from "FBN" package [1, 38]. To extract the G_{cc} seasonal trend of each community, we applied a cubic smoothing spline function on each filtered time series using the `gam` function of the "mgcv" package [53]. The smoothing parameter used for each time series was determined automatically by minimizing the generalized cross-validation score. We then implemented the method proposed by White et al. [48] in which green-up and green-down dates are determined by applying a threshold to the smoothing function. We used 50% of the rescaled greenness range as a threshold value. Green-up and green-down dates were found when G_{cc} increased above or decreased below the threshold value, respectively ([48], See Supplementary Fig. 3, Additional File 1). We defined the growing season length of each plant community as the number of days elapsed between the green-up and green-down dates. After removing time series that could not be used due to cameras malfunction, or modification to the field of view by wildlife (mostly moose and black bears), we ended up with 306 and 324 time series for green-up and green-down dates respectively and 286 complete time series that could be used to assess the growing season length (See supplementary Table 3, Additional File 1).

Statistical analyses

We performed a hierarchical partitioning of the variation to assess the contribution of Ecosystem identity and Community temporal variance, as well as Species richness, Community average functioning, and

Community asynchrony on the growing season phenology of plant communities. Specifically, we calculated the proportion of the total variance explained by each independent variable for each of the three phenology variables (green-up and green-down dates, and growing season length) using linear models and the `lm` function [31]. We introduced each independent variable successively to account for the hierarchical structure of our data: Ecosystem identity and Species richness, followed by Community temporal variance, Community average functioning and Community asynchrony, with the last three variables nested within Ecosystem identity (see Supporting information, for an example). Ecosystem identity and Species richness are part of the SAuVER experimental design and were fitted first. We determined the contribution of Species richness after removing the contribution of Ecosystem identity. We modelled Community temporal variance and Community average functioning (both nested within Ecosystem identity) using year identity (2013, 2014, 2015, 2016) and community identity (1:118), respectively (Fig. 1). Finally, we modelled Community asynchrony as the interaction between year and community identity, thus capturing the residual variation associated with the de-correlated temporal dynamics of plant assemblages within ecosystems (Fig. 1). We included all components as factors (unordered levels), with the exception of Species Richness (continuous scale). Partitioning of the variation in plant phenology was purely additive, such that the variance explained by the different components always sums to one. Including variables sequentially in the models may slightly underestimate the contribution of Community average functioning and Community asynchrony. However, fitting all terms simultaneously did not change the results, which indicated that there is no shared variation between variables.

At last, we directly tested whether plant Species richness increased the temporal stability (i.e., decreased year-to-year fluctuations) of plant phenology at the community level. This represents a standard test of the diversity-stability relationship at the level of plant communities. We used the coefficient of variation (CV) as a measure of instability [5, 40]:

$$CV=100 \times SD/Mean \quad \text{Equation 2}$$

where SD represents the standard deviation of a phenology variable within one community and Mean represents the arithmetic average across years over the 2013–2016 period. We used the average number of species observed within each unique plant community for the period 2013–2016 as our measure of Species richness for this analysis. We tested for a linear relationship between the plant species richness of a community and the CV of green-up and green-down dates. We excluded the fluvial marsh ecosystem from this analysis because we did not have four years of data for all communities. Linear models and hierarchical partitioning procedures were performed in R 3.4.0 [31].

Abbreviations

CV
Coefficient of variation

G_{cc}
Green chromatic coordinate index
G-D
Green-Down
GSL
Growing season length
G-U
Green-up
Sd
Standard deviation

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not Applicable

Availability of data and materials

All data generated or analysed during this study are included in this published article and its supplementary information files.

Competing interest

The authors declare that they have no competing interests.

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Author's contribution

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

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Figures

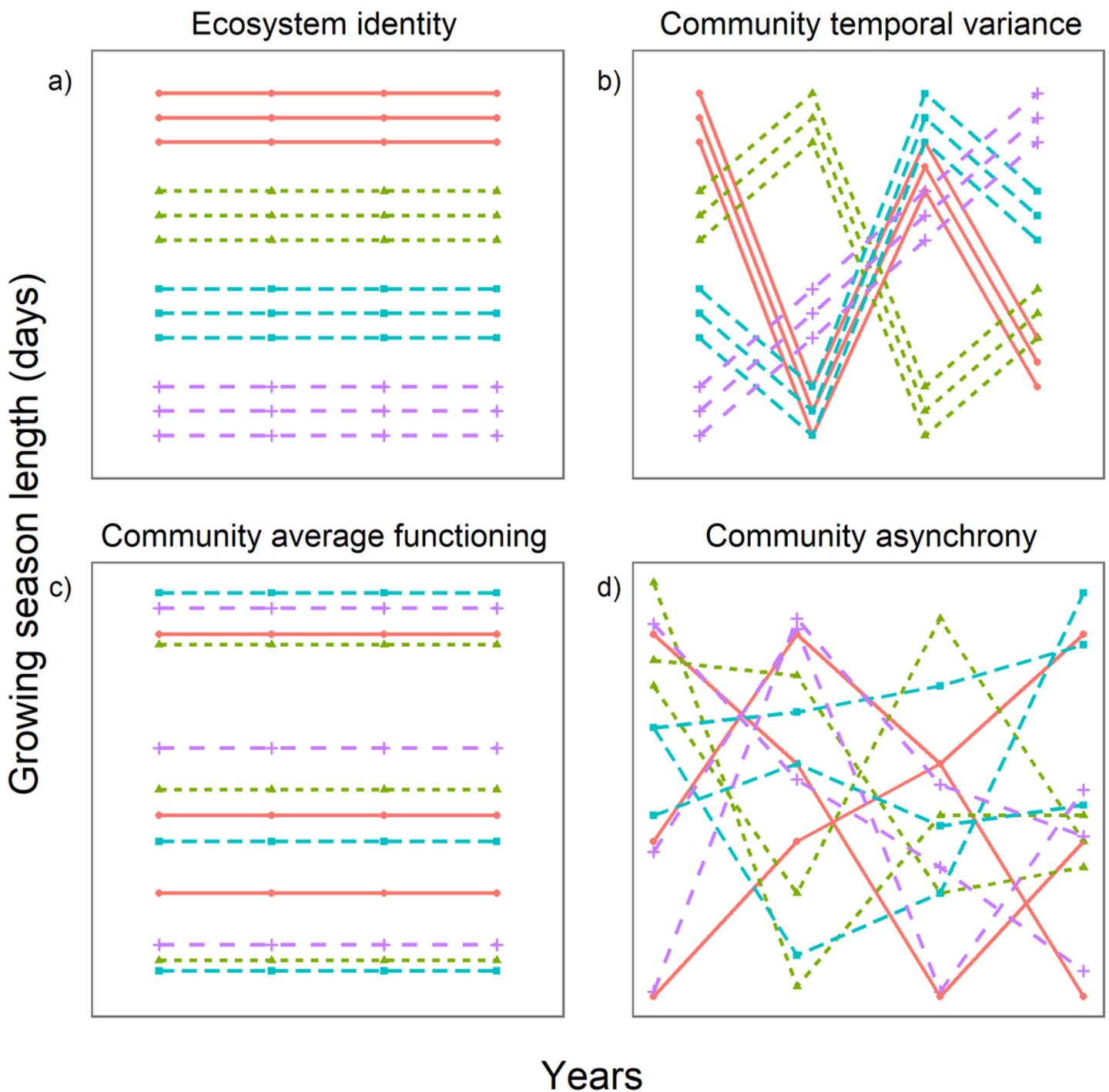


Figure 1

Contribution of different components to the growing season length of simulated plant communities in four ecosystems: (a) Ecosystem identity, (b) Community temporal variance, (c) Community average functioning and (d) Community asynchrony. In each scenario, the colors represent different ecosystems, each composed of 3 unique communities (plant assemblages). Each dot represents the growing season length of a unique community for a given year, whereas each line shows its inter-annual trend. Scenarios (a) and (b) are destabilizing because communities respond to the climatic and edaphic factors that

characterize each ecosystem each year, which increases variation in the growing season length among ecosystems. In contrast, scenarios (c) and (d) are stabilizing because the diversity of plant assemblages averages the variation among ecosystems. The percent of variation explained by one component is near 100% in each of the above scenarios

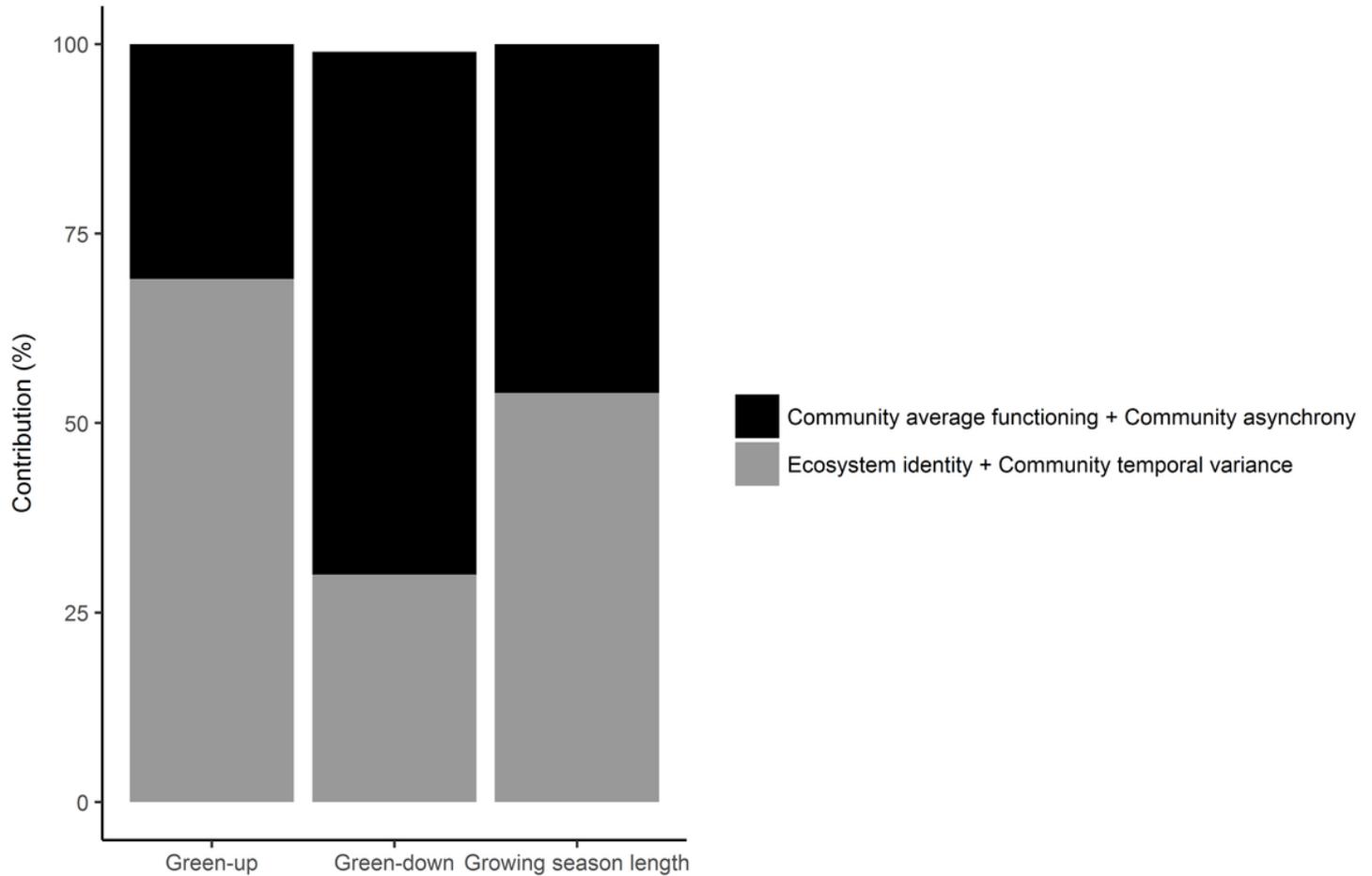


Figure 2

Percent relative contribution of the combined effect of Ecosystem identity and Community temporal variance (grey) and the combined effect of Community average functioning and Community asynchrony (black) to the green-up and green-down dates, as well as the growing season length of 118 plant communities.

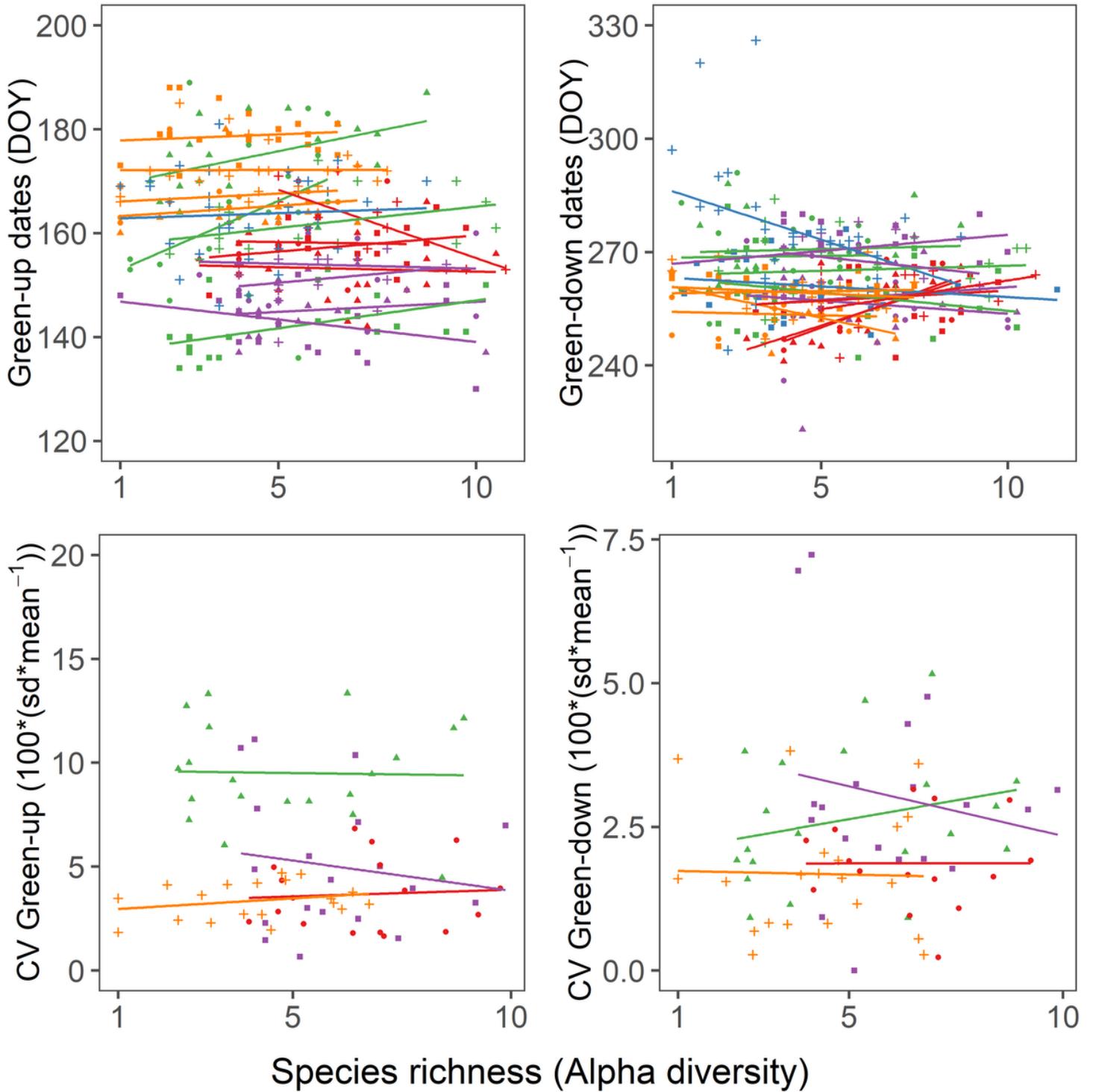


Figure 3

Species richness relationships to the Green-up (left) and Green-down (right) phenology of plant communities for every combination of year and ecosystem. Each dot represents the observed day-of-year (DOY) phenology of a unique plant community (top panels), or its temporal fluctuation (coefficient of variation; CV) across years (bottom panels). Each color represents a different ecosystem: Scirbi (Green), Maskinongé (Blue), Lac-à-la-Tortue (Purple), Bog-à-lanières (Red), Umiujaq (Orange). In the upper panels,

lines of the same color represent different years. In the lower panels, none of the relationships between plant species richness and inter-annual CV is statistically significant ($p > 0.05$, $R^2 < 0.01$).

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