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Author for correspondence:
Serguei Saavedra
e-mail: sersaa@mit.edu

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Structural stability as a consistent predictor of phenological events

Chuliang Song and Serguei Saavedra

Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Avenue, 02139 Cambridge, MA, USA

CS, 0000-0001-7490-8626; SS, 0000-0003-1768-363X

The timing of the first and last seasonal appearance of a species in a community typically follows a pattern that is governed by temporal factors. While it has been shown that changes in the environment are linked to phenological changes, the direction of this link appears elusive and context-dependent. Thus, finding consistent predictors of phenological events is of central importance for a better assessment of expected changes in the temporal dynamics of ecological communities. Here we introduce a measure of structural stability derived from species interaction networks as an estimator of the expected range of environmental conditions compatible with the existence of a community. We test this measure as a predictor of changes in species richness recorded on a daily basis in a high-arctic plant–pollinator community during two spring seasons. We find that our measure of structural stability is the only consistent predictor of changes in species richness among different ecological and environmental variables. Our findings suggest that measures based on the notion of structural stability can synthesize the expected variation of environmental conditions tolerated by a community, and explain more consistently the phenological changes observed in ecological communities.

1. Introduction

Phenological events typically refer to the timing of the first and last seasonal appearances of species in a given community [1,2]. These events follow temporal patterns that depend on several environmental variables, such as temperature, humidity, precipitation and day length, among others [3–6]. For example, the timing of the first seasonal appearance of pollinators and flowering plants have been well documented and observed to follow both temperature trends and day lengths very precisely [1,7,8]. In fact, strong changes in the environment can introduce significant changes to the phenology of species and impact the dynamics of a community. For instance, drastic phenological changes can generate a mismatch between the phenophase of interacting species and impact their life development [7,8]. While it has been shown that changes in the environment are linked to phenological changes [1,2,9,10], the direction of this link appears elusive and context-dependent [11–14]. Thus, finding consistent predictors of phenological events is of central importance for a better assessment of expected changes in the temporal dynamics of ecological communities [8,12].

Importantly, information about consistent predictors of phenological events may be embedded into the structure of species interaction networks. Indeed, early work has already suggested a strong relationship between the structure of interaction networks and phenological events [7,8,15–18]. This structure has been typically synthesized by who interacts with whom (or how species affect each other) in a given location and time. For example, focusing on mutualistic species, it is expected that phenological mismatches can be the strongest in species having both a weak and a brief dependency on other species [8]. Similarly, it has been shown that the flowering phenology of plant species can shift after loss of species from the community [17]. These relationships imply that the structure of interaction networks is a driving force of temporal dynamics in ecological communities and a potential indicator of phenological changes [19]. In fact, previous work has already shown a link between the structure of plant–pollinator networks and the natural variability of temperature present in a given location [20]. Thus, can the structure of interaction networks provide a consistent predictor of phenological events?

To answer the question above, we introduce a measure grounded on the notion of structural stability derived from interaction networks as an estimator of the expected range of environmental conditions compatible with the existence of a community. Structural stability is broadly defined as the capacity of a system to tolerate external perturbations without changing its qualitative behaviour [21], becoming a natural framework for the integration of community dynamics and environmental conditions [22,23]. Then, we apply this method to an empirical dataset recording the daily changes of environmental variables, plant–pollinator interactions, and the phenology of plants and pollinators during two spring seasons in a high-arctic community [19]. Finally, we perform a statistical analysis [24] to investigate the consistency of our measure of structural stability in explaining day-to-day changes in species richness, and to compare its performance against other ecological and environmental variables.

2. Methods

(a) Structural stability

We developed a measure based on the notion of structural stability to quantify the range of environmental conditions compatible with the existence of a community—what is known as feasibility [25]. This measure of structural stability of a feasible community is derived from a given interaction network and population dynamics model [22,26]. Because we are interested in studying a mutualistic system (plant–pollinator community), we approximated the community dynamics with a standard mutualistic dynamics model [19,26]. Formally, the dynamics of S interacting species are approximated by:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i + \sum_{j=1}^{S} a_{ij} N_i N_j,$$

where N_i corresponds to the abundance (or biomass) of species i, r_i is the intrinsic growth rate of species i, and a_{ij} are the elements of the interaction matrix $\boldsymbol{A}$ representing the interaction strength between species i and j ($i \neq j$), and a_{ii} is the self-regulation term of species i [27]. Note that our measure of structural stability is not restricted to the linear functional response assumed above as long as the dynamics are topologically equivalent [28].

Following previous work on mutualistic communities [19,26,29], the elements a_{ij} of the interaction matrix $\boldsymbol{A}$ can be estimated based on an observed interaction network $\boldsymbol{M}$, where each row i and column j corresponds to an observed plant and an observed pollinator species, respectively. Each binary element of this network $\boldsymbol{M}$ represents the presence ($m_{ij} = 1$) or absence ($m_{ij} = 0$) of an observed interaction between two species. The interaction matrix $\boldsymbol{A}$ is then constructed by estimating the interaction strength between a plant i and a pollinator j by $a_{ij} = \gamma m_{ij}/k_i^{\delta}$, where γ is the maximum level of mutualistic strength allowed by the community without losing dynamical stability [19], k_i is the number of direct interactions (mutualistic partners) of species i, and $\delta = 0.5$ is the mutualistic trade-off (values within $0 < \delta < 1$ lead to the same conclusions, see refs [19,26]). Note that γ fulfils an important normalization role. Because it is difficult to know the level of mutualistic strength in observed natural communities based on occurrence data only [30], γ systematically scales the level of strength as a function of community size (viz., species richness) [19,26]. We neglect intra-trophic competition in order to reduce the number of ad hoc free parameters in our study [19,31]. All the intra-specific interactions are set to $a_{ii} = -1$, which gives an equivalence between intrinsic growth rates r_i and carrying capacities K_i (recall that $K_i = -r_i/a_{ii}$). This implies that intrinsic growth rates can be directly translated into changes in the availability of resources as a function of environmental conditions [32–34].

Thus, to find the environmental conditions compatible with the existence of a community with a given interaction matrix $\boldsymbol{A}$, we calculated the parameter space of intrinsic growth rates leading to positive (feasible) species abundances [22,35]. This range of conditions (combination of intrinsic growth rates or carrying capacities) is called the feasibility domain D_F ($\boldsymbol{A}$) [26,36]. For example, heterotrophic species should exhibit smaller negative intrinsic growth rates than the benefits they can obtain from other species in order to have a positive balance of biomass (hence feasibility) [37,38]. This feasibility domain forms an algebraic cone [19, 36]:

$$D_F(\boldsymbol{A}) = \{\boldsymbol{r} = N_1^* \boldsymbol{v}_1 + \cdots + N_S^* \boldsymbol{v}_S, \text{ with } N_1^* > 0, \ldots, N_n^* > 0\},$$

where $\boldsymbol{N^*}$ are the species abundances at equilibrium. The size of the feasibility domain $D_F(\boldsymbol{A})$ over the Euclidean space $\mathbb{R}^{\mathbb{S}}$ can be calculated by the ratio of the following volumes [19,35]:

$$\Omega(\boldsymbol{A}) = \frac{\mathrm{vol}(D_F(\boldsymbol{A}) \cap \mathbb{B}^S)}{\mathrm{vol}(\mathbb{B}^S)},$$

where $\mathbb{B}^S$ is the unit sphere in dimension S (the normalized parameter space of intrinsic growth rates), representing the Euclidean space. Analytically, $\Omega(\boldsymbol{A})$ can be computed by [19,35]:

$$\Omega(\boldsymbol{A}) = \frac{1}{(2\pi)^{S/2}\sqrt{|\det(\Sigma)|}} \int \cdots \int_{\boldsymbol{N}^* \geq 0} \mathrm{e}^{-(1/2)\boldsymbol{N}^{*T} \Sigma^{-1} \boldsymbol{N}^*} \, \mathrm{d}\boldsymbol{N}^*,$$

where $\boldsymbol{A}^T \boldsymbol{A} = \frac{1}{2}\Sigma^{-1}$. The size $\Omega(\boldsymbol{A})$ of the feasibility domain can be efficiently computed via a quasi-Monte Carlo method for even relatively large communities [19,36]. The larger $\Omega(\boldsymbol{A})$, the larger the range of parameters of intrinsic growth rates compatible with positive species abundances in a given interaction matrix $\boldsymbol{A}$.

It is worth noting that $\Omega(\boldsymbol{A})$ is biased by the dimension S of the community [37]. That is, it decreases by increasing the community size—the volume of a unit ball approaches 0 as the dimension increases. Thus, we calculated the rescaled size of the feasibility domain as

$$\omega(\boldsymbol{A}) = \Omega(\boldsymbol{A})^{1/S}.$$

It can be proved that $\omega(\boldsymbol{A})$ is always between zero and one [38]. This measure of structural stability corresponds to the probability that a randomly chosen species in a given community can tolerate random environmental perturbations (see figure 1 for a graphical representation) [39–41]. In other words, this measure corresponds to the fraction of environmental conditions compatible with a feasible community given by a specific interaction matrix (estimated from an interaction network). Note that if we consider self-regulated non-interacting species, the value of structural stability would be $\omega(\boldsymbol{A}) = 0.5$. That is, the positive abundance of such species only depends on whether their intrinsic growth rate is positive (assuming that positive and negative values can happen with equal chance).

(b) Empirical data and statistical analysis

Next we investigated the role of our measure of structural stability in explaining phenological events, and compared its performance against other ecological and environmental variables. To address this, we used an empirical dataset recording daily changes in environmental conditions and plant–pollinator interactions in a high-arctic community during two spring seasons. This community was located at The Zackenberg Research Station in northeastern Greenland [19,42]. Species interactions between flowering plants and their pollinators were recorded on a daily basis for two consecutive years (in the springs of 1996 and 1997 whenever

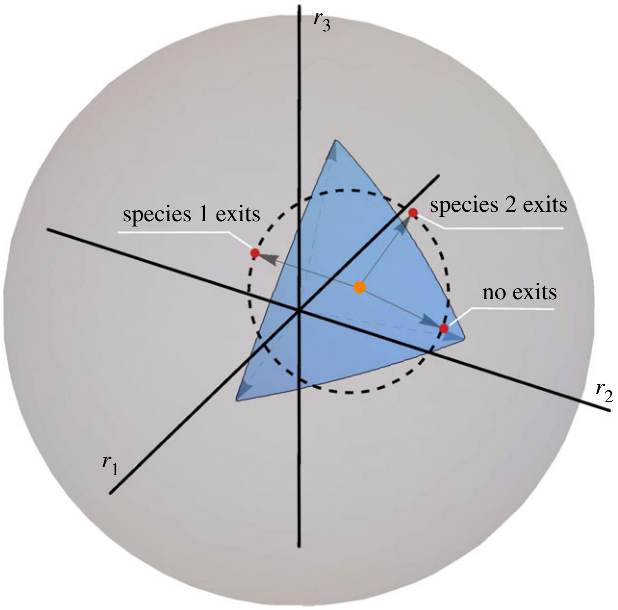

Figure 1. Graphical illustration of the structural stability of a feasible community. For a fictitious three-species community represented by an interaction matrix $\boldsymbol{A}$, the grey unit sphere corresponds to the normalized parameter space of intrinsic growth rates ($\boldsymbol{r} = [r_1, r_2, r_3]^{\mathrm{T}}$). Note that environmental conditions can be translated into the intrinsic growth rates of species. The blue cone represents the feasibility domain $D_F(\boldsymbol{A})$ generated by the column vectors of the interaction matrix $\boldsymbol{A}$, and represents the range of intrinsic growth rates compatible with a feasible community. For example, the orange symbol at the centre of the feasibility domain corresponds to a hypothetical starting environmental condition leading to a feasible community. The dashed circle corresponds to the hypothetical magnitude of an environmental change acting on the intrinsic growth rates of species. Each point along the circle corresponds to a possible direction of the environmental change. The red symbols on the circle outside the feasibility domain represent cases where at least one species exits the community (viz., species extinction). Therefore, without prior knowledge of the direction of the environmental change, we can use the relative size of the feasibility domain to estimate the probability of the existence of a community. (Online version in colour.)

weather allowed [42]). We compiled hourly measures of temperature and humidity of the sampled location for the entire observation period from the Greenland Ecosystem Monitoring Database. These hourly measures were used to calculate the mean temperature and mean humidity for each day in our observation period. Note that the means of these environmental variables are highly correlated to their variance. These two environmental variables were the most complete measurements captured over our observation period, and have been shown to be associated to temporal dynamics of plant–pollinator communities [2,8,20].

Data on species interactions allowed us to put together daily interaction networks $\boldsymbol{M}_t$, which we used to estimate daily interaction matrices $\boldsymbol{A}_t$ and to calculate the level of structural stability ω_t of the community for each observed day t. Because our measure of structural stability only provides average information (the probability) of species existence, we quantified the overall change in community size (change in species richness) for each day t by the difference (Δ_t) between the number of species present on a given day t and the number present on the previous day $t-1$. That is, values of $\Delta_t > 0$ indicate an increase of community size from day $t-1$ to day t, $\Delta_t < 0$ otherwise.

Then, we investigated the explanatory power of our measure of structural stability on the observed day-to-day changes in community size across the two seasons. This was carried out by using a standard principal component analysis (PCA) and a partial correlation analysis [43]. These two statistical analyses were performed by using the response variable at time t and all the predictor variables at time $t-1$. We used the (lagged) response variable at time $t-1$ as a predictor variable in order to provide a baseline for other predictor variables. Predictor variables include community size, structural stability, mean temperature and mean humidity. We scaled all variables (mean = 0, s.d. = 1) and detrended all variables by using the residual of a simple linear regression with time [24]. This process allowed us to avoid spurious correlations, and to discount the effect of other unknown temporal variables (e.g. day length) affecting the response variable [24]. The PCA was used to investigate the correlations and variance among changes in community size and the predictor variables across the two seasons. The partial correlation analysis was used to investigate the consistency of predictor variables across the two seasons in explaining the response variable while controlling for third variables [43].

3. Results

Focusing on the raw data (non-detrended and non-lagged variables), we confirmed that the assembly of the community follows a strong temporal pattern dictated by the natural sequence of days. Figure 2*a* shows that the daily number of species in the community generally increased as a function of the sequence of days (Spearman's rank correlations $r = 0.86$, $p = 0.001$ in first period; and $r = 0.61$, $p = 0.002$ in second period). However, figure 2*b* shows that changes in community size can move up or down regardless of the sequence of days (Spearman's rank correlations $r = -0.27$, $p = 0.231$ in first period; and $r = -0.37$, $p = 0.089$ in second period). This reveals that while community size has an increasing trend during the spring seasons, changes in community size vary on a day-by-day basis.

As expected, environmental and ecological variables appear to move in comparable directions to the assembly of the community. Figure 2*c* shows that the mean temperature increased as a function of the sequence of days (Spearman's rank correlations $r = 0.71$, $p = 0.001$ in first period; and $r = 0.649$, $p = 0.001$ in second period). In contrast, figure 2*d*,*e* shows that mean humidity and structural stability moved with no particular direction over the observation period (Spearman's rank correlations $r(h) = -0.16$, $p = 0.454$, $r(s) = -0.07$, $p = 0.752$ in first period; and $r(h) = 0.31$, $p = 0.168$, $r(s) = -0.07$, $p = 0.745$ in second period).

Focusing on the detrended and lagged variables, the PCA revealed that our measure of structural stability is a stronger predictor of changes in community size than all the other predictor variables. Figure 3 shows the PCA for the two seasons separately. The figure shows the strong relationship between structural stability and changes in community size under the two principal components derived from all our observed variables. The two components accounted for 61% and 67% of the variance in the first and second seasons, respectively. Note that the closer two vectors are in a PCA, the stronger their positive correlation.

Importantly, the partial correlation analysis revealed that our measure of structural stability is the only consistent predictor variable across all the different controls and seasons. Figure 4 shows all the different partial correlations between changes in community size and predictor variables controlling for each of the other predictor variables in turn. All the summary statistics can be found in electronic supplementary material, tables S1 and S2. The figure confirms that structural

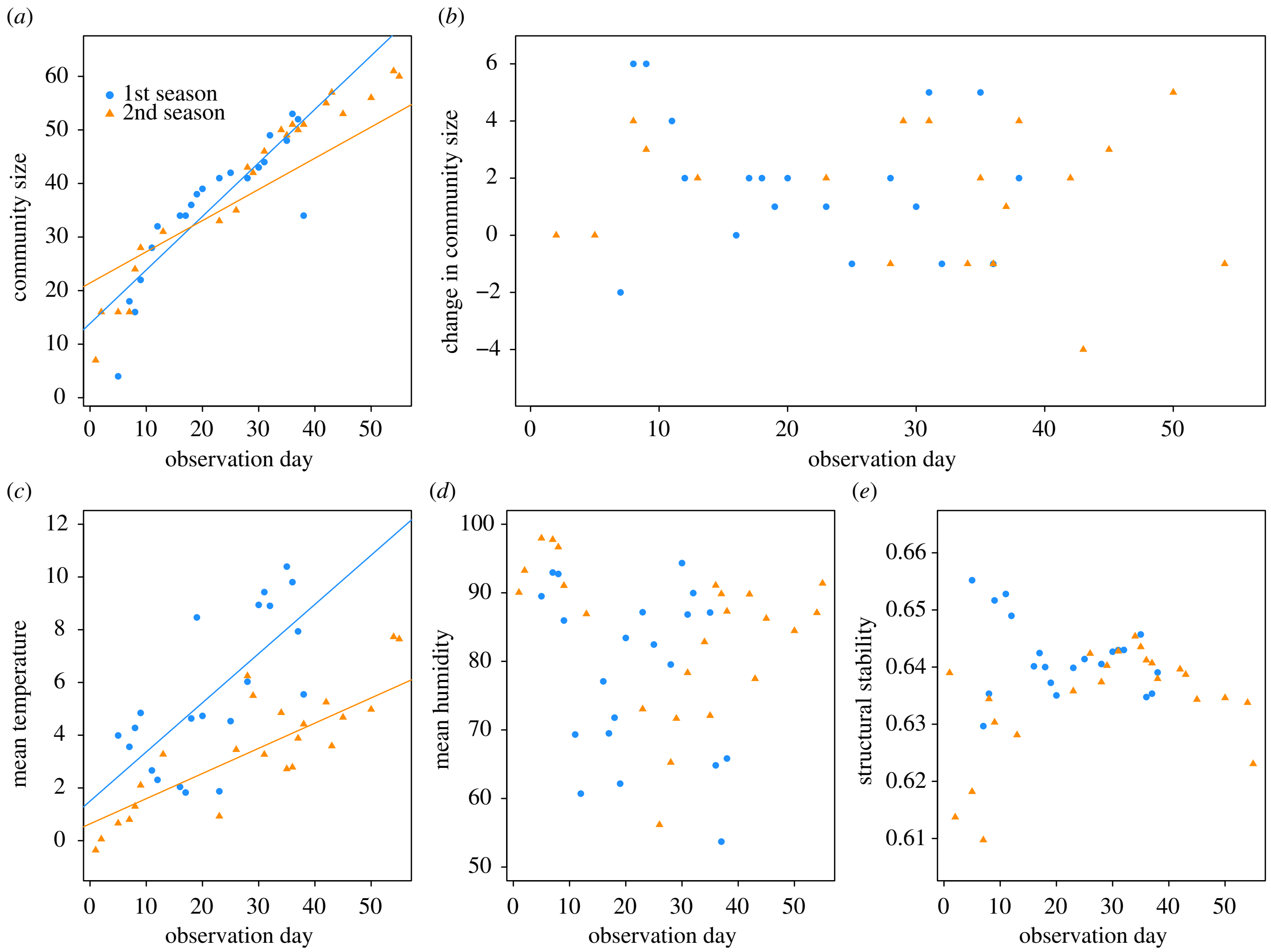

Figure 2. Environmental and ecological data in the observed plant–pollinator community across two spring seasons. For each day across the two observation periods (differentiated by symbols), (*a*) shows the community size (viz., species richness), (*b*) shows the changes in community size (difference between community size on a given day and the community size on the previous day), (*c*) shows the mean temperature, (*d*) shows the mean humidity and (*e*) shows the estimated structural stability derived from the observed interaction networks. Solid lines correspond to significant linear regressions between each of the variables and the sequence of observation days. Correlations are reported in the text. (Online version in colour.)

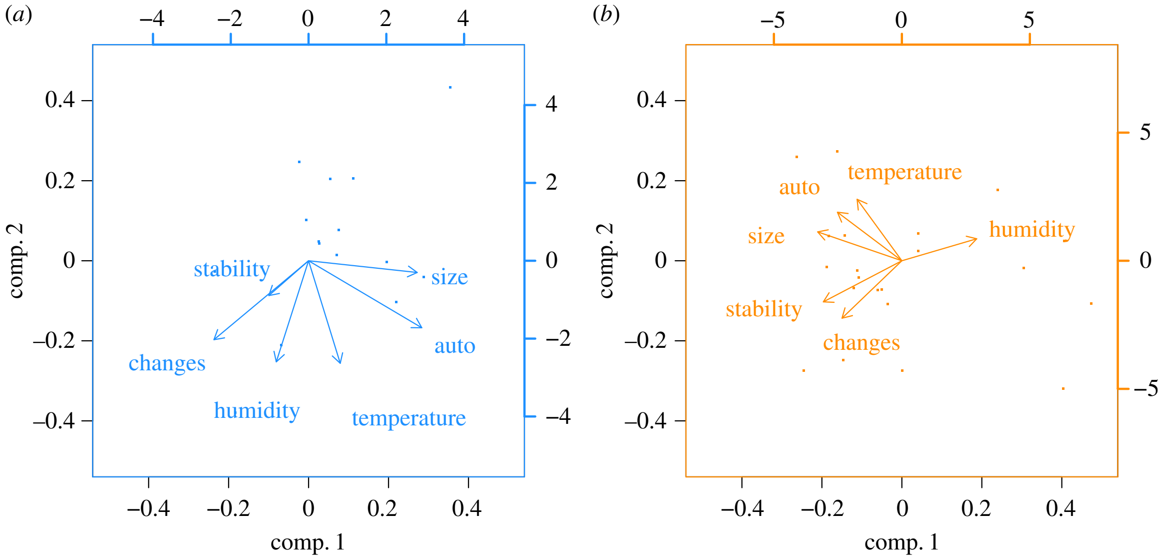

Figure 3. Correlation among changes in community size and predictor variables. Using a PCA, the figure shows the two principal components for changes in community size (the response variable) and predictor variables: community size, mean temperature, mean humidity and structural stability. All variables are detrended. All predictor variables are lagged by one day. Auto corresponds to the response variable lagged by one day. The arrows correspond to the six associated eigenvectors, and each small dot corresponds to one of the observation days. Note that the bottom and left axes correspond to the scaled values, whereas the top and right axes correspond to the vector loadings. (*a*,*b*) Correspond to the observations in the first and second seasons, respectively. Note that the closer two vectors are, the stronger their positive correlation. (Online version in colour.)

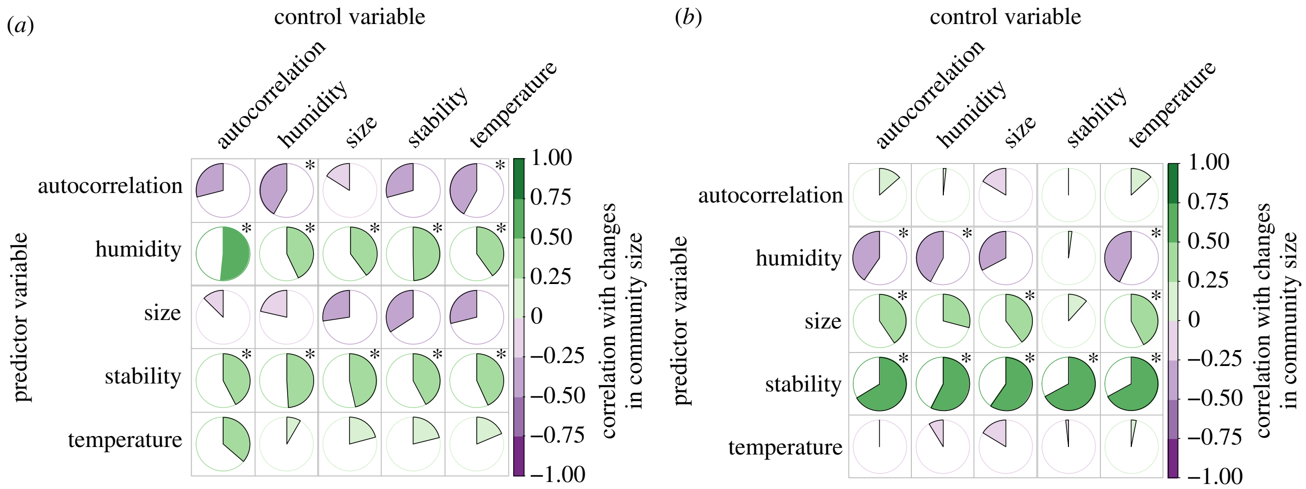

Figure 4. Structural stability as a consistent predictor of changes in community size. The figure shows the partial correlations between changes in community size (the response variable) and predictor variables (autocorrelation, mean humidity, community size, stability or mean temperature) while controlling for each of the other predictor variables in turn (columns). All variables are detrended. All predictor variables are lagged by one day. The fraction and the gradient of coloured symbols both represent the amount of correlation. Green and purple correspond to positive and negative correlations. The symbol * corresponds to correlations that are statistically significant at the 5% confidence level. Diagonal elements represent the simple correlation between changes in community size and a given predictor variable. (*a*,*b*) Correspond to the observations in the first and second seasons, respectively. Note that only structural stability has a consistent sign across all the different controls and seasons. (Online version in colour.)

stability is independent, highly, and positively correlated with changes in community size. Moreover, structural stability was the only predictor with a constant correlation sign across the two observation periods. These results were not found for any other predictor variable.

4. Discussion

Changing environmental conditions are the main drivers of ecological and evolutionary dynamics [11,32]. However, knowing how the specific combination of multiple environmental factors will affect the temporal dynamics of an ecological community is not trivial [12–14], especially under short-term time scales [2]. Here we have introduced a measure based on the notion of structural stability to estimate the range of environmental conditions (parameter space of intrinsic growth rates) compatible with a feasible community. This measure of structural stability was derived from interaction networks—one of the most abundant and reliable data there is about how species interact in a given location and time [30], which makes it applicable for other studies. Importantly, our results have shown that this measure is a consistent predictor of phenological events. While our data only cover two seasons and preclude us from making generalizations, the statistical analysis has confirmed theoretical expectations about the structural stability of feasible communities (i.e. the larger the structural stability of a community, the higher the probability of tolerating random perturbations).

This measure of structural stability provides an approximation to the level of external perturbations tolerated by a community. In this line, our results have illustrated that both environmental and ecological conditions are not enough to explain the short-term dynamics in ecological communities, it is also necessary to know the level of structural stability of the community under study at each point in time [23]. That is, environmental conditions alone are not informative of temporal dynamics unless they are paired with knowledge about the range of environmental conditions tolerated by a community. For instance, ecological memory (as a new research frontier) has been defined as the result of past environmental conditions and subsequent selection on populations encoded in the current structure of biological communities [11]. Thus, the structure of interaction networks can be the result of the interplay between internal constraints and an environmental filtering, encoding the tolerance of a community to its environment and subsequent dynamics of its population. Hence, our measure of structural stability derived from interaction networks may be associated with the ecological memory of a community. Future work should test these ideas more systematically on larger data sets spanning multiple years and recording multiple environmental factors.

Phenological events are short-term dynamics by definition. However, our findings suggest that this seasonal assembly should not be conceptualized as a result of daily weather conditions only. For example, the persistence of mutualistic systems depends on the matching of mutually beneficial interactions between species and should also be the result of the combination between ecological and environmental factors over long periods of time [11]. In this line, our measure of structural stability links environmental conditions and long-term population dynamics of feasible communities (positive abundances at equilibrium). While it is unlikely that ecological communities are at equilibrium, feasibility conditions should be interpreted only as descriptors of the dynamical space in which a community is evolving [44]. Moreover, feasibility is a necessary condition for species persistence regardless of whether the communities are at equilibrium or not [45]. Therefore, phenological events can be understood as a seasonal steady state [46], where it might be possible to use analytically derived time-dependent probability distributions to explain and anticipate them. Thus, our tools can be a promising route toward this goal.

We must point out that we cannot disentangle whether the patterns (and therefore the results) that we have observed across the two seasons are the consequence of a bias in the sampling process or the actual ecological dynamics acting on this high-arctic community. To properly disentangle these effects it is necessary to have more seasons and environmental variables. For example, the plant–pollinator community that we have studied was subject to relatively low anthropogenic disturbances [42], and it is unclear whether structural stability should play a constant and major role under more disturbed conditions [20,23]. In other words, future work should examine under which conditions the role of structural stability becomes undermined by the effect of daily stochastic fluctuations.

Data accessibility. The data and R-code supporting the results are archived on Github (http://github.com/clsong/PRSB-Song_Saavedra-2018).

Authors' contributions. S.S. designed and supervised the study. C.S. performed the study. Both authors wrote the manuscript.

Competing interests. We declare we have no competing interests.

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References

1. Forrest JRK, Thomson JD. 2011 An examination of synchrony between insect emergence and flowering in rocky mountain meadows. *Ecol. Monogr.* **81**, 469–491. (doi:10.1890/10-1885.1)
2. Rafferty NE, CaraDonna PJ, Burkle LA, Iler AM, Bronstein JL. 2013 Phenological overlap of interacting species in a changing climate: an assessment of available approaches. *Ecol. Evol.* **3**, 3183–3193. (doi:10.1002/ece3.668)
3. Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M. 2002 Ecological effects of climate fluctuations. *Science* **297**, 1292–1296. (doi:10.1126/science.1071281)
4. Walther GR. 2010 Community and ecosystem responses to recent climate change. *Phil. Trans. R. Soc. B* **365**, 2019–2024. (doi:10.1098/rstb.2010.0021)
5. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B. 2014 Defaunation in the Anthropocene. *Science* **345**, 401–406. (doi:10.1126/science.1251817)
6. Scheffers BR *et al.* 2016 The broad footprint of climate change from genes to biomes to people. *Science* **354**, aaf7671. (doi:10.1126/science.aaf7671)
7. Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland O. 2009 How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **12**, 184–195.doi:10.1111/j.1461-0248.2008.01269.x
8. Rafferty NE, CaraDonna PJ, Bronstein JL. 2015 Phenological shifts and the fate of mutualisms. *Oikos* **124**, 14–21. (doi:10.1111/oik.01523)
9. Hance T, van Baaren J, Vernon P, Boivin G. 2007 Impact of extreme temperatures on parasitoids in a climate change perspective. *Annu. Rev. Entomol.* **52**, 107–126. (doi:10.1146/annurev.ento.52.110405.091333)
10. Mazer SJ, Gerst KL, Matthews ER, Evenden A. 2015 Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. *Ecosphere* **6**, 1–27. (doi:10.1890/ES14-00433.1)
11. Thompson JN *et al.* 2001 Frontiers of ecology. *Bioscience* **51**, 16–23. (doi:10.1641/0006-3568(2001)051[0015:FOE]2.0.CO;2)
12. Power DA, Watson RA, Szathmáry E, Mills R, Powers ST, Doncaster CP, Czapp B. 2001 Frontiers of ecology. *Biol. Direct* **10**, 16–23.
13. Agrawal AA *et al.* 2007 Filling key gaps in population and community ecology. *Front. Ecol. Environ.* **5**, 145–152. (doi:10.1890/1540-9295(2007)5[145:FKGIPA]2.0.CO;2)
14. Sheldon KS, Huey RB, Kaspari M, Sanders NJ. 2018 Fifty years of mountain passes: a perspective on Dan Janzen's classic article. *Am. Nat.* **191**, 553–565. (doi:10.1086/697046)
15. Price MV, Waser NM. 1998 Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* **79**, 1261–1271. (doi:10.1890/0012-9658(1998)079[1261:EOEWOP]2.0.CO;2)
16. Dunne JA, Harte J, Taylor KJ. 2003 Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecol. Monogr.* **73**, 69–86. (doi:10.1890/0012-9615(2003)073[0069:SMFPRT]2.0.CO;2)
17. Wolf AA, Zavaleta ES, Selmants PC. 2017 Flowering phenology shifts in response to biodiversity loss. *Proc. Natl Acad. Sci.* **114**, 3463–3468. (doi:10.1073/pnas.1608357114)
18. CaraDonna PJ, Petry WK, Brennan RM, Cunningham JL, Bronstein JL, Waser NM, Sanders NJ. 2017 Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecol. Lett.* **20**, 385–394. (doi:10.1111/ele.12740)
19. Saavedra S, Rohr RP, Olesen JM, Bascompte J. 2016 Nested species interactions promote feasibility over stability during the assembly of a pollinator community. *Ecol. Evol.* **6**, 997–1007. (doi:10.1002/ece3.1930)
20. Song C, Rohr RP, Saavedra S. 2017 Why are some plant-pollinator networks more nested than others? *J. Anim. Ecol.* **86**, 1417–1424. (doi:10.1111/1365-2656.12749)
21. Thom R. 1972 *Stabilité structurelle et morphogenèse*. Paris, France: InterÉditions.
22. Saavedra S, Rohr RP, Bascompte J, Godoy O, Kraft NJB, Levine JM. 2017 A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* **87**, 470–486. (doi:10.1002/ecm.1263)
23. Cenci S, Song C, Saavedra S. 2017 Rethinking the importance of the structure of ecological networks under an environment-dependent framework. *BioRxiv*. (doi:10.1101/219691)
24. Iler AM, Inouye DW, Schmidt NM, Hoye TT. 2017 Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity. *Ecology* **98**, 647–655. (doi:10.1002/ecy.1690)
25. Roberts A. 1974 The stability of a feasible random ecosystem. *Nature* **251**, 607–608. (doi:10.1038/251607a0)
26. Rohr RP, Saavedra S, Bascompte J. 2014 On the structural stability of mutualistic systems. *Science* **345**, 1253497. (doi:10.1126/science.1253497)
27. Case TJ. 2000 *An illustrated guide to theoretical ecology*. Oxford, UK: Oxford University Press.
28. Cenci S, Saavedra S. 2018 Structural stability of nonlinear population dynamics. *Phys. Rev. E* **97**, 012401. (doi:10.1103/PhysRevE.97.012401)
29. Saavedra S, Rohr RP, Dakos V, Bascompte J. 2013 Estimating the tolerance of species to the effects of global environmental change. *Nat. Commun.* **4**, 2350. (doi:10.1038/ncomms3350)
30. Schupp EW, Jordano P, Gómez JM. 2017 A general framework for effectiveness concepts in mutualisms. *Ecol. Lett.* **20**, 577–590. (doi:10.1111/ele.12764)
31. Cenci S, Montero-Castañ A, Saavedra S. 2017 Estimating the effect of the reorganization of interactions on the adaptability of species to changing environments. *J. Theor. Bio.* **437**, 115–125. (doi:10.1016/j.jtbi.2017.10.016)
32. Levins R. 1968 *Evolution in changing environments: some theoretical explorations*. Princeton, NJ: Princeton University Press.
33. Vandermeer JH. 1975 Interspecific competition: a new approach to the classical theory. *Science* **188**, 253–255. (doi:10.1126/science.1118725)
34. Cadotte MW, Tucker CM. 2017 Should environmental filtering be abandoned? *Trends Ecol. Evolut.* **32**, 429–437. (doi:10.1016/j.tree.2017.03.004)
35. Ribando MJ. 2006 Measuring solid angles beyond dimension three. *Discrete Comput. Geom.* **36**, 479–487. (doi:10.1007/s00454-006-1253-4)
36. Genz A, Bretz F. 2009 *Computation of multivariate normal and T probabilities*, vol. 195. Berlin, Germany: Springer Science and Business Media.
37. Grilli J, Adorisio M, Suweis S, Barabás G, Banavar JR, Allesina S, Maritan A. 2017 Feasibility and coexistence of large ecological communities. *Nat. Commun.* **8**, 14389. (doi:10.1038/ncomms14389)

38. Song C, Rohr RP, Saavedra S2018A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *J. Theor. Biol.* **450**, 30 – 36. (doi:10.1016/j.jtbi.2018.04.030)
39. Saavedra S, Rohr RP, Gilarranz LJ, Bascompte J. 2014 How structurally stable are global socioeconomic systems? *J. R. Soc. Interface* **11**, 20140693. (doi:10.1098/rsif.2014.0693)
40. Rohr RP, Saavedra S, Peralta G, Frost CM, Bersier L-F, Bascompte J, Tylianakis JM. 2016 Persist or produce: a community trade-off tuned by species evenness. *Am. Nat.* **188**, 411 – 422. (doi:10.1086/688046)
41. Saavedra S, Cenci S, del Val E, Boege K, Rohr RP. 2017 Reorganization of interaction networks modulates the persistence of species in late successional stages. *J. Animal Ecol.* **86**, 1136 – 1146. (doi:10.1111/1365-2656.12710)
42. Olesen JM, Stefanescu C, Traveset A. 2011 Strong, long-term temporal dynamics of an ecological network. *PLoS ONE* **6**, e26455. (doi:10.1371/journal.pone.0026455)
43. Legendre P, Legendre L. 2012 *Numerical ecology*, 3rd edn. Amsterdam, The Netherlands: Elsevier.
44. Lewontin RC. 1969 The meaning of stability. *Brookhaven Symp. Biol.* **22**, 13 – 24.
45. Hofbauer J, Sigmund K. 1998 *Evolutionary games and population dynamics*. Princeton, NJ: Princeton University Press.
46. Strauss SY, Webb CO, Salamin N. 2006 Probabilistic model predicts dynamics of vegetation biomass in a desert ecosystem in NW China. *Proc. Natl Acad. Sci. USA* **114**, E4944 – E4950. (doi:10.1073/pnas.1703684114)