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# Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence

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**Abstract.** Many of the observed species interactions embedded in ecological communities are not permanent, but are characterized by temporal changes that are observed along with abiotic and biotic variations. While work has been done describing and quantifying these changes, little is known about their consequences for species coexistence. Here, we investigate the extent to which changes of species composition impact the likelihood of persistence of the predator–prey community in the highly seasonal Białowieża Primeval Forest (northeast Poland), and the extent to which seasonal changes of species interactions (predator diet) modulate the expected impact. This likelihood is estimated extending recent developments on the study of structural stability in ecological communities. We find that the observed species turnover strongly varies the likelihood of community persistence between summer and winter. Importantly, we demonstrate that the observed seasonal interaction changes minimize the variation in the likelihood of persistence associated with species turnover across the year. We find that these community dynamics can be explained as the coupling of individual species to their environment by minimizing both the variation in persistence conditions and the interaction changes between seasons. Our results provide a homeostatic explanation for seasonal species interactions and suggest that monitoring the association of interactions changes with the level of variation in community dynamics can provide a good indicator of the response of species to environmental pressures.

**Key words:** Białowieża Primeval Forest; coexistence; ecological networks dynamics; food webs; homeostasis; predator–prey systems; structural stability.

## INTRODUCTION

Empirical evidence has revealed that networks of interspecific interactions are not permanent (Margalef 1968, de Ruiter et al. 2005). Longitudinal studies have reported that ecological communities change not only their species composition across short and long timescales, but also the identity and strength of their interspecific interactions. Typically, these changes are observed along with seasonal environmental variation or an environmental gradient (Houlahana et al. 2007). For instance, in different trophic communities sampled across multiple years and seasons, studies have detected significant changes in species composition, percentages of diet consumption, number of interspecific interactions, and predator–prey ratios (Baird and Ulanowicz 1989, Schoenly and Cohen 1991, Tavares-Cromar and Williams

1996, Thompson and Townsend 1999, Hart and Stone 2000). Host–parasitoid and host–parasite communities have also been found to vary in both their interspecific interactions and species functional roles, to which can be attributed to temporal changes in species body size (Laliberté and Tylianakis 2010, Pilosof et al. 2013). Similarly, it has been well documented that the timing and length of species phenophase can lead to short- and long-term interaction changes in mutualistic communities (Alarcón et al. 2008, Olesen et al. 2008, 2011, Petanidou et al. 2008, Carnicer et al. 2009, Díaz-Castelazo et al. 2010, Burkle et al. 2013).

While much work has been done looking at the description and quantification of interaction changes in ecological communities (see Poisot et al. [2012], for an extensive review of the literature), thus far, there is little agreement about both the driving mechanisms and the consequences of interaction changes for species coexistence (Carstensen et al. 2014, Vizentin-Bugoni et al. 2014, Olito and Fox 2015, Trojelsgaard et al. 2015). Yet, understanding these effects is of paramount importance in order to face future community-wide risk scenarios of extinctions (Tylianakis et al. 2008, Saavedra et al. 2013).

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Focusing on ecological communities subject to environmental variations, ecological theory suggests that the impact of seasonal changes can make a community to switch between different levels of maturity or development (e.g., seasonal differences in species composition; Margalef 1963). In particular, recurrent or periodic changes can preclude ecological communities from moving in a one-directional line of succession, and as a result, these communities can be typically found in an intermediate point in their developmental sequence. Estuaries, intertidal zones, and freshwater marshes are good examples of such communities, where species life histories are intimately coupled to the environmental periodicity (Odum 1969). Because of this expected coupling, seasonal changes of species interactions are also expected to keep the community under a homeostatic state, i.e., under small variations in the conditions compatible with species coexistence despite changes of species composition in the community (Odum 1969, Ernest and Brown 2001).

To test the above hypothesis and to investigate any association between seasonal changes of species interactions and species coexistence, we study the seasonal dynamics of the terrestrial vertebrate predator–prey community in the Białowieża Primeval Forest (northeast Poland). Between summer and winter, this community shows an important species turnover and changes in species interactions (predator diet). Using a general predator–prey model (Case and Casten 1979, Logofet 1993, Rossberg 2013), we study the derived likelihood of community persistence as a function of both the network of species interactions and the changes in the community. This likelihood is estimated following a structural stability framework (Thom 1972, Alberch and Gale 1985, Stone 1988, Bastolla et al. 2005, 2009, Rohr et al. 2014) and recent developments in the application of feasibility analysis to ecological (Svirezhev and Logofet 1983, Logofet 1993, Rohr et al. 2014) and non-ecological systems (Saavedra et al. 2014). In particular, we investigate the extent to which the difference in species composition in Białowieża impacts the likelihood of persistence of the predator–prey community across the year, and the extent to which seasonal changes in species interactions modulate the expected impact.

## MATERIAL AND METHODS

### *Empirical data*

Białowieża represents the last old-growth temperate primeval forest in Europe, where seasonality is the organizing theme of the environment. The climate is continental with Atlantic influence, and two main seasons, cold and warm, are mainly distinguished (Jędrzejewska and Jędrzejewski 1998). Accordingly, predator diet has been often investigated separately in spring–summer (April–September) and in autumn–winter (October–March). For simplicity, we refer to them throughout the text as summer

and winter, respectively. Winters can include periods of deep snow cover and extremely cold temperatures. The mean snow cover is 10 cm, although in some winters it has reached up to 96 cm and covered the ground from November until April. The temperature in January, the coldest month, averages  $-4.8^{\circ}\text{C}$ . June, July, and August are the warmest months with mean daily temperatures of  $17^{\circ}\text{C}$ , and the highest insolation, on average 7 h/d compared to 48 min/d in December (Jędrzejewska and Jędrzejewski 1998). Importantly, as expected, the strong seasonality in environmental conditions brings together an equally important species turnover between summer and winter (Jędrzejewska and Jędrzejewski 1998). Further details about the study area are provided in Appendix S1.

### *Community characterization*

We characterized the community formed by predators (carnivores and raptors) and their prey in the Białowieża Primeval Forest (northeast Poland) during the summer and winter seasons. Species presence and their interactions for the two seasons were compiled from 15 published studies covering two or more years mostly within the period 1985–1996 (see Appendix S1). Data are available in Data S1. In total, we observed 21 and 17 predators in summer and winter, respectively. All predators present in winter were also present in summer. We also observed 128 and 127 prey in summer and winter, respectively. From a total of 141 prey consumed across the two seasons, only 114 were consumed in both seasons. Species that are present across the entire year are called permanent species (e.g., black species in Fig. 1), otherwise they are called seasonal species (e.g., colored species in Fig. 1). This species turnover generated a summer ( $N^S$ ) and a winter ( $N^W$ ) predator–prey interaction network with seasonal species, and coupled by a subset of permanent species (see Fig. 1).

Importantly, interactions between permanent species were also changing between summer and winter. From a total of 435 interactions observed among permanent species, 303 were present in both seasons (e.g., black interactions in Fig. 1), 62 in summer only (e.g., orange interactions in Fig. 1), and 70 in winter only (e.g., blue interactions in Fig. 1). This reveals that there is an important number of seasonal changes of interactions among permanent species that can be coupled to the environmental variations in Białowieża Primeval Forest.

### *Community dynamics*

To investigate the dynamics in the Białowieża predator–prey community in each season, we followed a general consumer–resource framework (Levins 1968, MacArthur 1970, Case and Casten 1979). Traditionally, this framework has been used to develop reasonable explorations of predator–prey systems, while allowing the behavior of these systems to be analytically tractable

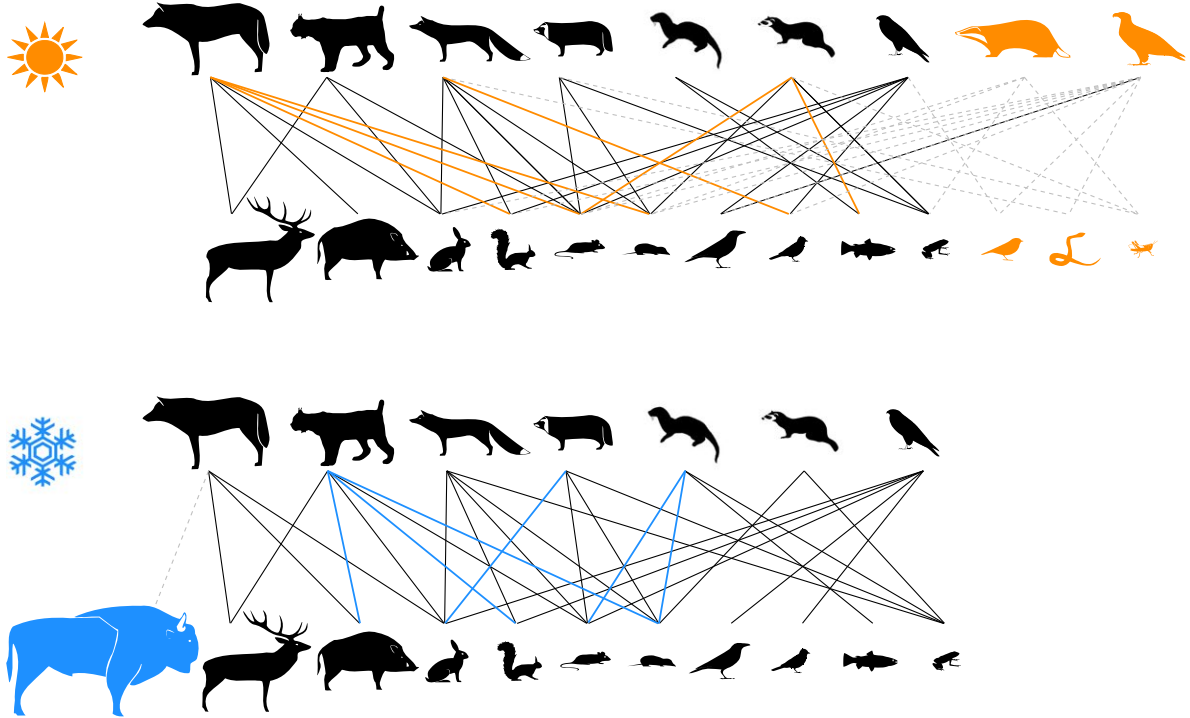


FIG. 1. Illustration of the Białowieża Forest predator–prey community in summer and winter. The top and bottom figures correspond, respectively, to a subsample of the summer and winter predator–prey interaction networks (see Appendix S1 for a matrix representation of the complete interaction networks). In each interaction network, predators are at the top and prey at the bottom. Species in black and color correspond, respectively, to permanent and seasonal species. Black and colored lines correspond to interactions among permanent species that are present the entire year (permanent interactions) and in one season only, respectively. Dashed lines represent interactions either between permanent and seasonal species or among seasonal species only. Permanent predators are wolf (*Canis lupus*), lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), otter (*Lutra lutra*), polecat (*Mustela putorius*), and Northern Goshawk (*Accipiter gentilis*). Summer predators are Eurasian badger (*Meles meles*) and Lesser-spotted Eagle (*Aquila pomarina*). Permanent prey are red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), hare (*Lepus europaeus*), squirrel (*Sciurus vulgaris*), mouse and vole (Muridae, Arvicolidae), shrew (Soricidae), thrush (*Turdus* sp.), resident small passerine bird (Passeriformes), fish (Cyprinidae), and amphibian (Amphibia). Summer prey are migratory small passerine bird (Passeriformes), reptile (Reptilia), and insect (Coleoptera). Winter prey, European bison (*Bison bonasus*).

and depend to a lesser extent on unknown parameters (Case and Casten 1979, Svirezhev and Logofet 1983, Logofet 1993, Rossberg 2013). We described the dynamics of our predator–prey (consumer–resource) system by a general Lotka–Volterra model given by the following set of ordinary differential equations:

$$\frac{dC_i}{dt} = C_i \left( -m_i + \epsilon_i \sum_k \gamma_{ki} R_k \right) \quad (1a)$$

$$\frac{dR_k}{dt} = R_k \left( \alpha_k - R_k - \sum_i \gamma_{ki} C_i \right) \quad (1b)$$

where  $C_i$  denotes the biomass of predator (consumer)  $i$ ,  $R_k$  denotes the biomass of prey  $k$  (resource),  $m_i$  is the mortality rate of predator  $i$ , and  $\alpha_k$  is the intrinsic growth rate of prey  $k$ . Following previous work,  $\epsilon_i$  is the standard conversion efficiency of predator  $i$  and is set to  $\epsilon_i = 0.1$  (Rossberg 2013).

Additionally,  $\gamma_{ki}$  denotes the trophic interaction strength between prey  $k$  and predator  $i$ . We did not include intraguild predation because this is not observed in the data. For the sake of generalization and according to observations (Margalef 1968, Saavedra et al. 2013), we assumed that trophic interaction strengths are parameterized by  $\gamma_{ki} = \gamma_0 / d_k^\delta$  when prey  $k$  is consumed by predator  $i$ , and  $\gamma_{ki} = 0$  otherwise. The parameter  $\gamma_0$  represents the overall level of trophic interaction strength in the community. The variable  $d_k$  denotes the number of predators consuming prey  $k$ , and  $\delta$  is a scalable resource-partition parameter that modulates the consumption strength of prey  $k$  among its predators. For each season, the elements  $\gamma_{ki}$  are derived from the summer ( $N^S$ ) and the winter ( $N^W$ ) predator–prey interaction network accordingly (see Fig. 1). Because the resource-partition parameter assumes a symmetric partition of prey's biomass among their predators, we also explored how asymmetric partitions affect our results (see Appendix S2).

### Likelihood of community persistence

To investigate the likelihood of persistence of a predator–prey community, we studied the range of parameter space in the dynamical system (Eq. 1) leading to positive and stable biomasses for all species. The larger the range of parameter space compatible with positive stable solutions ( $C_i^* > 0$  and  $R_k^* > 0$ ), the larger the likelihood that the observed community can persist (Rohr et al. 2014, Saavedra et al. 2014).

Because we are interested in positive stable solutions, first we needed to find the conditions leading to stability in the given system when subject to perturbations in species biomass. Following Case and Casten (1979), the dynamical system of Eq. 1 does not have alternative stable states under a very large range of assumptions on its parameter values. It has been shown that for such dynamical systems, we can construct a Lyapunov function, which is a mathematical sufficient condition to constrain the dynamical system to converge to a single globally stable equilibrium point ( $C^*$ ,  $R^*$ ). This implies that the dynamical system will absorb any perturbation in biomass and the system will eventually return to a globally stable equilibrium point. Therefore, the only question that remains to be answered is whether this predator–prey system can converge into positive stable equilibrium points, i.e., an equilibrium point with  $C_i^* > 0$  and  $R_k^* > 0$ .

The conditions for having positive globally stable equilibrium points, once the interaction strengths have been fixed ( $\gamma_{ki}$  and  $\epsilon_i$ ), are dictated only by both the mortality rates of predators ( $m_i$ ) and the intrinsic growth rates of prey ( $\alpha_k$ ). The set of vectors  $[\mathbf{m}, \boldsymbol{\alpha}]$  compatible with stable persistence are the ones that make the solution of the following system of linear equations strictly positive:

$$\mathbf{m} = \text{diag}(\boldsymbol{\epsilon})\boldsymbol{\gamma}'\mathbf{R} \quad (2a)$$

$$\boldsymbol{\alpha} = \mathbf{R} + \boldsymbol{\gamma}\mathbf{C}, \quad (2b)$$

where  $\boldsymbol{\gamma}$  is the matrix of trophic-interaction strengths. This set of vectors, called the feasibility domain (Logofet 1993, Rohr et al. 2014, Saavedra et al. 2014), is given by

$$D_F = \{m_i = \epsilon_i \gamma_{1i} x_1 + \dots + \epsilon_i \gamma_{S_R i} x_{S_R} \text{ and } \alpha_i = x_i + \gamma_{i1} y_1 + \dots + \gamma_{iS_C} y_{S_C} \mid \text{with } x_i > 0 \text{ and } y_i > 0\}. \quad (3)$$

Importantly, this feasibility domain is never empty: it is always possible to choose values for  $m_i$  and for  $\alpha_k$  such that we obtain a positive solution ( $C_i^* > 0$  and  $R_k^* > 0$ ). For instance, we can set  $m_i = \epsilon_i \sum_k \gamma_{ki}$  and  $\alpha_k = R_k + \sum_i \gamma_{ki}$ , and the corresponding positive stable point is given by  $R_k^* = 1$  and  $C_i^* = 1$ . This example stresses the importance of not only looking at whether the system can reach a positive solution, but also at how large the feasibility domain is (how big the set of vectors leading to a positive stable solution is). The larger the feasibility domain, the larger the likelihood of stable persistence.

Building on previous work looking at competition systems (Svirezhev and Logofet 1983, Logofet 1993), the size of the feasibility domain for predator–prey systems given by Eq. 1 can be estimated by the following formula (see Appendix S3 for further details):

$$\Omega(\boldsymbol{\gamma}) = \frac{|\det(\mathbf{A})|}{\prod_j (\sum_i A_{ij})} \quad (4)$$

where the matrix  $\mathbf{A}$ , with its elements  $A_{ij}$ , is a two-by-two block matrix, function of  $\boldsymbol{\gamma}$ , given by

$$\mathbf{A} = \begin{bmatrix} \text{diag}(\boldsymbol{\epsilon})\boldsymbol{\gamma}' & 0 \\ \mathbf{I} & \boldsymbol{\gamma} \end{bmatrix} \quad (5)$$

where  $\mathbf{I}$  is the identity matrix. This formula can be interpreted as the probability that a vector  $[\mathbf{m}, \boldsymbol{\alpha}]$  sampled uniformly at random (under the only constraint of being positive and with a fixed sum) falls within the feasibility domain. Therefore, the measure  $\Omega(\boldsymbol{\gamma})$  can be used as a quantification of the likelihood of community persistence in summer and winter by using the corresponding matrix of trophic-interaction strengths ( $\boldsymbol{\gamma}$ ) for each season.

Importantly, each likelihood  $\Omega(\boldsymbol{\gamma})$  is a function of the overall trophic-interaction strength ( $\gamma_0$ ) present in each season. For instance, for a value of  $\gamma_0 = 0$  (no trophic interactions) predators cannot survive and consequently the likelihood of community persistence is zero. We found that the relationship between interaction strength and the likelihood of persistence is characterized by a concave function, meaning that there is a value of interaction strength ( $\gamma_i$ ) at which the likelihood of persistence is maximized (see Appendix S4: Fig. S1). Because we do not have the empirical data to infer  $\gamma_0$ , we decided to use  $\gamma_0 = \gamma_i$  in order to calculate the maximum likelihood of community persistence for each season. Note that in order to calculate  $\gamma_0$ , we would require to have data on the amount of each prey biomass consumed by each predator. Importantly, the value of  $\gamma_0$  does not change the qualitative results of our study (see Appendix S4: Fig. S1). All calculations are performed using Matlab software version 2014a (The Mathworks, Inc. Natick, MA, USA). Code in Matlab and R software are provided in Data S1.

### Expected likelihood of community persistence

The expected likelihood of community persistence in a given season is evaluated from randomly-generated interaction networks. For each season, the only difference between the observed and randomized networks is the identity (not the number) of interactions among permanent species. These interactions in the randomized networks are randomly sampled from a meta network. Following ecological studies showing that many species interactions are forbidden due, for example, to phenological or morphological differences between species (Jordano et al. 2003, Vázquez 2005, Olesen et al. 2010), the meta network is simply the source of all possible



interactions that can be established between species according to our data. See Appendix S4: Fig. S2 for an illustrative example of the meta network and randomizations. For each randomized network, we calculated the corresponding likelihood of community persistence as explained in the previous subsection. Using these likelihoods, we generated a distribution of expected likelihood of community persistence in summer and winter accordingly.

#### *Observed variation in likelihood of community persistence*

To calculate the variation in the likelihood of community persistence between the observed summer and winter network, we used the log absolute difference defined by  $\log(\Delta(\Omega)) = |\log(\Omega(\gamma^s)) - \log(\Omega(\gamma^w))|$ , where  $\Omega(\gamma^s)$  and  $\Omega(\gamma^w)$  are the likelihood of community persistence for summer and winter, respectively.

#### *Expected variation in likelihood of community persistence*

To calculate the variation in the likelihood of community persistence between a randomized summer and winter network, we used pairs of randomized summer and winter networks that share a given number of interactions among permanent species. The observed summer and winter networks share 303 species interactions. Thus, we generated randomized summer and winter networks as in the previous subsection, we selected pairs of randomized summer and winter networks that share 303 interactions, we calculated their corresponding likelihood of community persistence as in the previous subsection, and we computed the variation in their likelihood as explained also in the previous subsection. Using these variations, we generated a distribution of expected variation in

likelihood of community persistence. See Appendix S4: Fig. S3 for an illustrative example of these randomizations.

## RESULTS

### *Effect of species turnover on community persistence*

We find that the observed seasonal species turnover (i.e., differences in species composition) makes any potential combination of predator–prey interactions in the community to have a lower likelihood of persistence  $\Omega(\gamma)$  in summer than in winter. Fig. 2 shows that the observed predator–prey community has a lower likelihood of persistence in summer (orange line) than in winter (blue line). Fig. 2 also reveals that the distribution of expected likelihood values generated by 50 000 randomized winter interaction networks (right histogram) is always higher than the distribution of expected likelihood values generated by 50 000 randomized summer interaction networks (left histogram). In other words, there are no such potential seasonal changes of species interactions that can compensate for the seasonal species turnover and keep the likelihood of persistence exactly invariant across the year. This shows that the likelihood of community persistence is strongly linked to the species composition present in the community.

Additionally, these findings show that, in summer, the observed likelihood of persistence is large relative to the expected values within that season, while in winter, the likelihood is relatively small. We can interpret this result as a possible expression of an intermediate point in the developmental sequence of this community. As the species composition strongly fluctuates between summer and winter, the community may be pushed to maintain a closer connection between the resulting seasonal sub-communities.

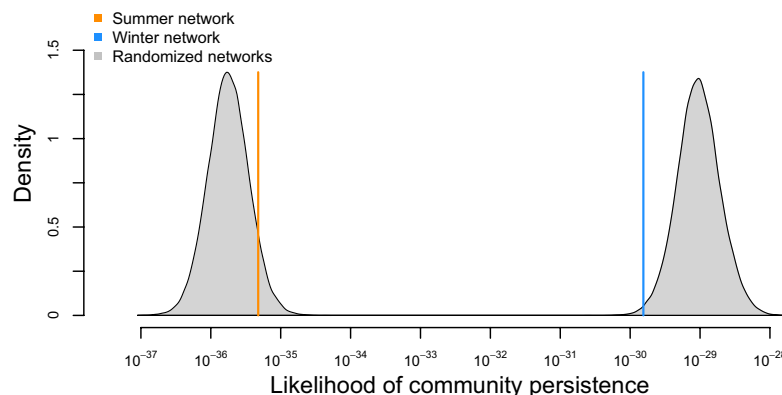


FIG. 2. Species turnover impact the likelihood of persistence across seasons. The orange line (left) and blue line (right) show the observed persistence likelihood ( $\gamma$ ) in summer and winter, respectively. The left and right histograms correspond, respectively, to the expected persistence likelihood in summer and winter. Expected persistence likelihood values are generated from potential randomized interaction networks. The figure is generated using a resource-partition parameter  $\delta = 1$ . Other values generate qualitatively similar results (see Appendix S4: Figs. S4 and S5).

### *Effect of seasonal interaction changes on community persistence*

To investigate whether the observed seasonal species interactions modulate the impact of species turnover on the likelihood of community persistence, we measure how the observed variation in the likelihood of community persistence between summer and winter compares to the expected variations. We compare the observed variation to the situation where the number of randomly generated permanent interactions is equal to the number of observed permanent interactions, and to the situation where there would be no interaction changes whatsoever. Because we do not know the direction of change in the data, i.e., from summer to winter or vice versa, we study both possibilities to eliminate interaction changes. The elimination of summer-to-winter change is generated by replacing all the interactions among permanent species in the winter network with the ones observed during summer. The elimination of winter-to-summer change is generated in the opposite way. The expected variation in the likelihood of persistence for the no change situation is then calculated between the summer (winter) network and the non-changed winter (summer) network.

Fig. 3 shows that the observed variation in the likelihood of community persistence  $\log(\Delta(\Omega))$  (black/left line) is smaller than 99% of 100 000 pairs of randomly-generated expected variations (histogram). Similarly, Fig. 3 shows that the observed variation is smaller than the expected variations generated from no interaction changes whatsoever (colored lines). These results reveal that the observed seasonal changes of species interaction minimize the variation in the likelihood of community persistence associated with species turnover across seasons.

### *Coupling of species to seasonal variations*

To explain the community dynamics above, we analyze the extent to which individual species can be coupled to their seasonal environmental variations. Theory purports that mutual information between current and future states can reduce unnecessary changes that are energetically costly for species (Margalef 1963, Odum 1969). In this context, the fewer the changes in both the persistence conditions and the number of interaction changes, the higher the mutual information between seasons, and in turn, the higher the coupling between individual species and their environment.

To explore the above hypothesis, we quantify the extent to which the variation in the likelihood of community persistence changes as function of the number of permanent interactions. Specifically, we compare the differences in the expected variations (e.g., see histograms of Fig. 3) when changing the number of randomly-generated permanent interactions between seasons. In the observed predator–prey community, 365 is the maximum possible number of permanent interactions

between seasons, which is given by the seasonal network with the fewest number of interactions among permanent species (summer network). On the other hand, 70 is the minimum possible number of permanent interactions, which is given by the difference between the total number of interactions among permanent species (in both summer and winter) and the number of interactions among permanent species in summer. Recall that the observed number of permanent interactions is 303. Therefore, we vary the number of randomly generated permanent interactions between 70 and 365.

We hypothesize that if lower expected variations would result from a larger number of permanent interactions than the observed number of permanent interactions, it would reveal unnecessary interaction changes in the Białowieża community. If much higher expected variations would result from a lower number of permanent interactions than the observed number, it would reveal a sub-optimized variation. Otherwise, it would reveal that species have indeed a strong coupling with the seasonality of their environment.

We find that all the distributions of expected variations, as function of the number of randomly generated shared interactions, can be well approximated by a Gaussian distribution, and are characterized by the same

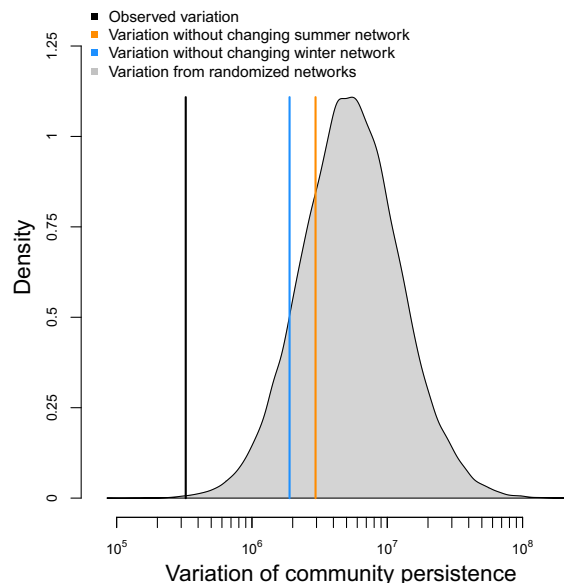


FIG. 3. Seasonal changes of species interactions modulate the variation in the likelihood of community persistence. The black line (left) corresponds to the observed variation in the likelihood of persistence between summer and winter (derived from Fig. 2). The histogram corresponds to the population of expected variations in the likelihood of persistence from all potential pairs of randomized interaction networks in summer and winter that share 303 predator–prey interactions. The orange (right) and blue (middle) lines correspond, respectively, to the variation in the likelihood of persistence that would be expected in the scenario without interaction changes from summer to winter and vice versa. The figure is generated using a resource-partitioning parameter  $\delta = 1$ . Other values generate qualitatively similar results (see Appendix S4: Figs. S6 and S7).

mean (within 0.1% of variation) but not by the same variance. This implies that the variance can be used as an indicator of how low or high the expected variation can move as function of the number of permanent interactions.

Fig. 4 shows that the larger the number of permanent interactions (viz., the smaller the number of interaction changes), the smaller the variance from the mean, and therefore, the larger the expected variations between seasons. In fact, as soon as we increase the number of permanent interactions from the observed value (dashed line in Fig. 4), the variance exponentially drops. In contrast, decreasing the number of permanent interactions from the observed value can only marginally increase this variance. This reveals that the observed number of interaction changes sets the balance between reaching a low variation in the likelihood of community persistence and preserving a large number of permanent interactions between seasons.

### DISCUSSION

Ecological communities subject to abiotic and biotic variations have been typically characterized by temporal

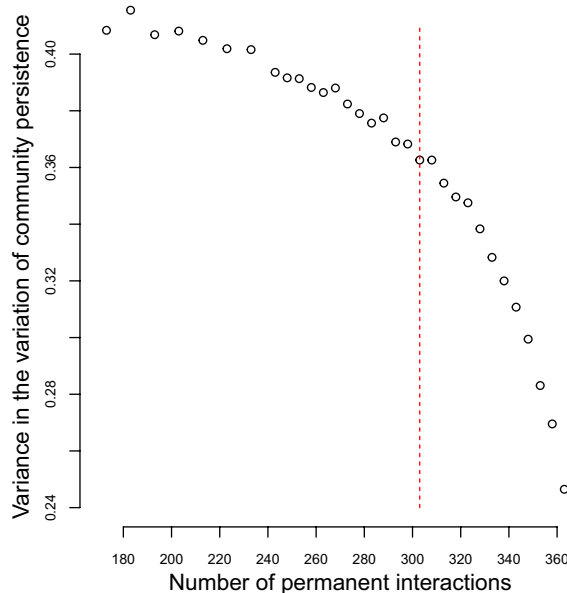


FIG. 4. Community balance between number of permanent interactions and variation in the likelihood of persistence. The figure shows the variance in the expected variation in likelihood of community persistence as function of the number of permanent interactions used to generate the randomized summer and winter networks. The mean value of the expected variation is the same (within 0.1% of variation) across all the different number of permanent interactions. The dashed line corresponds to the observed number (303) of permanent interactions. Note that the larger the number of permanent interactions (i.e., the smaller the number of interaction changes), the smaller the variance of the expected variation (i.e., the lower the chances of reaching a low variation). The figure is generated using a resource-partition parameter  $\delta = 1$ . Other values generate qualitatively similar results (see Appendix S4: Figs. S8 and S9).

changes of interspecific interactions. Unfortunately, many of the consequences of these interaction changes are still poorly understood. To shed new light into these factors, we have studied the seasonal dynamics of the predator–prey community in the highly seasonal Białowieża Primeval Forest. Between summer and winter, this community shows an important species turnover and changes of predator diet. We have found that the observed species turnover generates a difference in the likelihood of community persistence across seasons regardless of any potential change of predator–prey interactions. Importantly, we have shown that the observed interaction changes minimize the variation in the likelihood of persistence across the year. These results support ecological theory suggesting that seasonal species interactions play a key role in maintaining a homeostatic state or a relatively low level of dynamical variation on ecological communities despite changes in species composition (Margalef 1968, Odum 1969, Ernest and Brown 2001).

Additionally, ecological theory suggests that simple rules of energetics and information can be governing the dynamics of ecological communities (Margalef 1963, Odum 1969, de Ruiter et al. 2005). Here, we have shown that seasonal changes of species interactions are coupled to the environment by minimizing both the variation in persistence conditions and unnecessary dietary changes that can be energetically costly for individual species. Therefore, the observed community dynamics should not be understood as group selection, where the behavior of individual species would be expected to follow a common goal for all species. Under a group-selection framework, interaction changes would be an explicit mechanism of the entire community to achieve the goal of maintaining a low variation in the likelihood of persistence. In contrast, the intimate coupling between interaction changes and environmental seasonality can be simply the result of a long-term adaptation process on each of the individual species coping with seasonal changes and reducing unnecessary energetic costs.

By using a well-defined and parsimonious dynamical model, our findings represent a clear example of how seasonal changes of species interactions can have regulating effects on community persistence. This suggests that the adaptation of biological species to changing environmental conditions partially depends on their capacity to adjust their interspecific interactions. If interaction changes are slower or faster than the effects of environmental change, ecological communities may exhibit stronger fluctuations. While more detailed dynamical models can be incorporated, we advocate for the range of conditions leading to the stable coexistence of species as a potential quantitative measure of the likelihood of community persistence. We believe that monitoring the association of species interactions changes with the level of dynamical variation on ecological communities can provide a good indicator of the response of species to environmental pressures.



Finally, our results raise a number of interesting questions about the extent to which changes of species interactions along seasonal variations or environmental gradients should generate different consequences on ecosystem functioning. A potential hypothesis would be that relatively undisturbed ecological communities subject to seasonal or periodic environmental changes should exhibit relatively low variation in the likelihood of persistence across time. In contrast, under anthropogenically generated changes or changes over an environmental gradient, ecological communities should exhibit relatively high variation in the likelihood of persistence. Such a hypothesis would be congruent with simulated effects of directional changes on ecological communities (Saavedra et al. 2013), the expected effects of global environmental change (Tylianakis et al. 2008), and requires further exploration.

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#### LITERATURE CITED

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-1013.1/supinfo>

# Appendix S1 from S. Saavedra et al., “Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence”

## Empirical Data

We compiled diet data of the ecological community formed by predators (carnivores and raptors) and their prey in the Polish side of the Białowieża Primeval Forest. The predator-prey interaction network was built based on 15 published studies on predator diet in the area covering more than one year, mostly from the period 1985-1996 (reviewed by Jędrzejewska and Jędrzejewski (1998), see Section Study Area for a complete list of references). Detailed information on predator diet, specifically presence/absence of prey (considering prey as any food item consumed by a predator), was obtained for 21 predator species, and used to build the network of predator-prey interactions in summer and winter (the list of predators is provided in section Study Area). The winter network included only 17 of these predators since the other four are absent or inactive in winter (the lesser-spotted eagle *Aquila pomarina*, the hobby *Falco subbuteo*, the honey buzzard *Pernis apivorus*, and the Eurasian badger *Meles meles*). We did not consider predator species occurring in low-densities, occasional in the study area, or associated to human settlements. Few cases of intraguild predation were excluded. As we wanted to build a forest network, data from the ecotone with surrounding farmland was also excluded.

Predator diet (predator-prey interactions) was evaluated from the analysis of either scats



or pellets, and either from prey or their remains collected in the field. They were often collected under raptor nest during the breeding season, and with the help of snow- and radio-tracking in the case of carnivores. The diet of five raptors (the northern goshawk *Accipiter gentilis*, the sparrowhawk *Accipiter nisus*, the Tengmalm's owl *Aegolius funereus*, the long-eared owl *Asio otus*, and the pygmy owl *Glaucidium passerinum*) and two carnivores (the least weasel *Mustela nivalis*, and stoat *Mustela erminea*) was available only in one season. In those cases, we took a conservative approach of considering that the diet in the other season was the same (with the exception of insects, which were excluded from the winter network). We carried additional robustness tests in which we removed those seven predators from the analysis, and found that our results remain qualitatively the same (results not shown).

In the case of prey categories that could only be determined by the genus (or higher category) level, we proceeded as follows: (1) when all or most species of the genus were present in the predator diet (e.g. *Apodemus flavicollis*, *A. sylvaticus* in the red fox *Vulpes vulpes* diet), we did not include the genus category (e.g. *Apodemus* sp.) as an additional prey because it is quite likely that the unidentified specimens under the genus category would belong to one of the prey species already included. This helped us to avoid biases in the number of prey species; (2) when only the genus category was present in the published data (e.g. *Apodemus* sp. in the common buzzard *Buteo buteo* diet), we attributed it to the most abundant species (e.g. *A. flavicollis*), or leave it as the class, family or genus category (e.g. *Gastropoda* sp., *Lumbricidae* sp. or *Anas* sp.). We tried to minimize the presence of categories of undetermined birds, amphibians, rodents, bats, reptiles, insects by assigning to the most abundant species when possible. The insects present in the diet were grouped into several categories: Coleoptera, Hymenoptera, Odonata, Trichoptera and Lepidoptera. Some prey were merged under one single general

category, such as fleshy fruits, tree seeds, grasses or mushrooms. Carcasses of ungulates, both wild and domestic, were all aggregated under the same category. Predator-prey interactions in summer and winter are provided in Appendix S5.

## Study Area

Białowieża Primeval Forest (ca 1500 km<sup>2</sup>) is located in the Polish-Belarusian borderland. It is the last primeval temperate forest of its size in lowland temperate Europe and represents a biodiversity hotspot and a reference for biological studies (Jędrzejewska and Jędrzejewski, 1998). Due to centuries of protection as a royal forest, it remained until the beginning of the 20th century practically unmanaged. It is located in the nemoral-boreal transition zone. Although the area is flat (135-202 m.a.s.l.) the forest is very diverse and numerous forest types are distinguished. Oak-lime-hornbeam forest (*Quercus robur* — *Tilia cordata* — *Carpinus betulus*), coniferous, and mixed forest dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* are the most abundant. Alderwoods and wet areas are dominated by European alder *Alnus glutinosa* and European ash *Fraxinus excelsior*. Open areas include river meadows, clearings inside the forest, and village glades. Old-growths of natural origin cover an important part of the forest (ca 44%) (Faliński, 1986; Jędrzejewska and Jędrzejewski, 1998).

The area under study is inhabited by a rich animal community. Among others, more than 9280 insects, 178 breeding birds, and 58 species of mammals have been recorded. This high diversity is observable also at very local scales. For instance, 74 bird species bred in a 33-ha patch of forest over a 30-year period. Forty species of raptors and carnivores have been reported occurring in the area (Jędrzejewska and Jędrzejewski, 1998). Carnivores and raptors of the temperate lowland forests of Europe coexist with nearly 200 species of other terrestrial vertebrates that are their potential prey. They belong to 7 major animal

groups: invertebrates, fish, amphibians, reptiles, birds, small, and medium-sized mammals and ungulates. About 3 quarters of the animals living in the forest are amphibians, 15% are mammals, and 9% are birds. The ungulate community, which makes up 83% of the crude biomass of all potential prey, is represented by 5 species: European bison *Bison bonasus*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa*. Large carnivores are represented by the Eurasian lynx *Lynx lynx* and the wolf *Canis lupus* (Jędrzejewska and Jędrzejewski, 1998). The declaration of World Heritage Site by UNESCO has been recently enlarged to the whole forest.

Species presence and their interactions for the two seasons were compiled from 15 published studies covering two or more years mostly within the period 1985-1996 (see table S1).



| Predator species                | Study years                     | Period        | Reference  |
|---------------------------------|---------------------------------|---------------|--|
| <i>Accipiter gentilis</i>       | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Accipiter nisus</i>          | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Buteo buteo</i>              | 1986-1994                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (1994 <i>b</i> )                       |
| <i>Pernis apivorus</i>          | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998); van Manen (2003)   |
| <i>Aquila pomarina</i>          | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Falco subbuteo</i>           | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Strix aluco</i>              | 1985-1992                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (1994 <i>b, a</i> )                    |
| <i>Glaucidium passerinum</i>    | 1989, 1993-1994                 | spring-summer | Jędrzejewska and Jędrzejewski (1998, 1993)   |
| <i>Aegolius funereus</i>        | 1993-1994                       | spring-summer | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Asio otus</i>                | 1967, 1969, 1983                | spring-summer | Jędrzejewska and Jędrzejewski (1998); Ruprecht and Szwagrzak (1987)                              |
| <i>Lynx lynx</i>                | 1985-1995                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (1993 <i>b</i> ); Okarma et al. (1997) |
| <i>Canis lupus</i>              | 1985-1996                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (2000)                                 |
| <i>Vulpes vulpes</i>            | 1985-1989                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski and Jędrzejewska (1992)                       |
| <i>Nyctereutes procyonoides</i> | 1986-1995                       | year round    | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Meles meles</i>              | 1986-1995                       | spring-summer | Jędrzejewska and Jędrzejewski (1998); Goszczyński et al. (2000)                                  |
| <i>Martes martes</i>            | 1985-1992                       | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (1993 <i>c</i> )                       |
| <i>Mustela erminea</i>          | 1987-1988                       | autum-winter  | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Mustela nivalis</i>          | 1961-1991, 1989-1991, 1990-1991 | autum-winter  | Jędrzejewska and Jędrzejewski (1998)   |
| <i>Mustela putorius</i>         | 1987-1989, 1986-1991            | year round    | Jędrzejewska and Jędrzejewski (1998); Jędrzejewski et al. (1993 <i>a</i> )                       |
| <i>Lutra lutra</i>              | 1988-1996                       | year round    | Brzeziński et al. (1993); Jędrzejewska et al. (2001)   |
| <i>Mustela vison</i>            | 1987-1995                       | year round    | Jędrzejewska et al. (2001)   |

Table S1: List of predator species for which information on their diets was collected to build the network. Diets were collected from the forest habitats in the Polish part of the Białowieża Primeval Forest. The references, study time, and material used are provided.

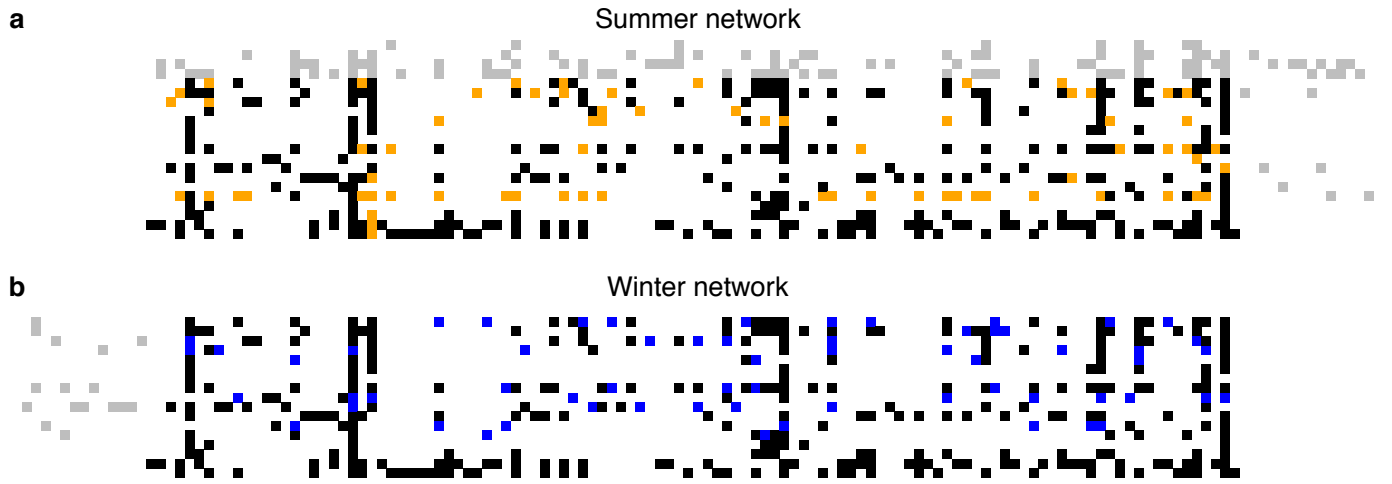


Figure S1: Matrix representation of the Białowieża predator-prey community in summer and winter. The top and bottom figures correspond respectively to the complete summer and winter predator-prey interaction networks. In each network, predators are represented by rows and prey by columns. Black and colored symbols correspond to interactions that are present in both seasons and in one season only, respectively. Gray symbols represent interactions either between seasonal and permanent species or among seasonal species only.

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# Appendix S2 from S. Saavedra et al., “Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence”

## Exploration of asymmetric parameterizations of interaction strengths

In the absence of appropriate empirical data to field parameterize the trophic-interaction strength of the predator-prey community, we explore how asymmetric randomized interaction strengths affect our results. Note that appropriate data would be to have the amount of each prey biomass consumed by each predator. We assume that the trophic-interaction strengths follow the parameterization given by

$$\gamma_{ki} = \gamma_0 w_{ki} \text{ when prey } k \text{ is consumed by predator } i \text{ and } \gamma_{ki} = 0, \text{ otherwise} \quad (\text{S1})$$

where  $\gamma_0$  is the overall level of trophic-interaction strength, and  $w_{ki}$  are randomly assigned weights. The values of  $w_{ki}$  are assumed to follow a log-normal distribution:

$$w_{ki} \sim \text{log-Normal}(\mu = 0, \sigma^2), \quad (\text{S2})$$

of mean  $\mu = 0$  and variance  $\sigma^2$ . Note that without loss of generality, we can set the mean to zero ( $\mu = 0$ ) because it is a multiplicative factor that can always be corrected by  $\gamma_0$ .

We explore different randomizations of  $w_{ki}$  by the following procedure. First, for each

trophic link in summer and winter, we sample randomly  $w_{ki}$ . This generates a set of weights for the winter and summer networks. Second, using the same procedure as in the main text, we generate alternative networks by re-sampling the trophic interactions. Third, we assign weights to the trophic interactions of the generated-networks (step 2) by sampling randomly in the set of  $w_{ki}$  generated during the first step. Fourth, as in the main text, we compute the observed and expected variations in the likelihood of persistence. Finally, we compute the fraction of expected variations in the likelihood of persistence that are larger than the observed variation. We repeat this five-step procedure 200 times with four different levels of variance ( $\sigma = 0.2, 0.4, 0.6, 0.8$ ).

Figure S1 shows that for a low level of variance ( $\sigma < 0.6$ ) in the parameterization of  $w_{ki}$  we obtain the same results as in the main text, i.e., the expected variations in the likelihood of persistence between randomized networks are almost always larger than the observed variation. In contrast, with high levels of variance, it becomes more difficult that the observed variation is significantly lower than the expected variations. However, this is not a surprising pattern. Indeed, it is expected that in any system, there must be a threshold, where the effect of network architecture will be relatively smaller than the effect of the weights. Further work should explore whether trophic-interaction strengths that suppress the effect of networks architecture can be biologically plausible.

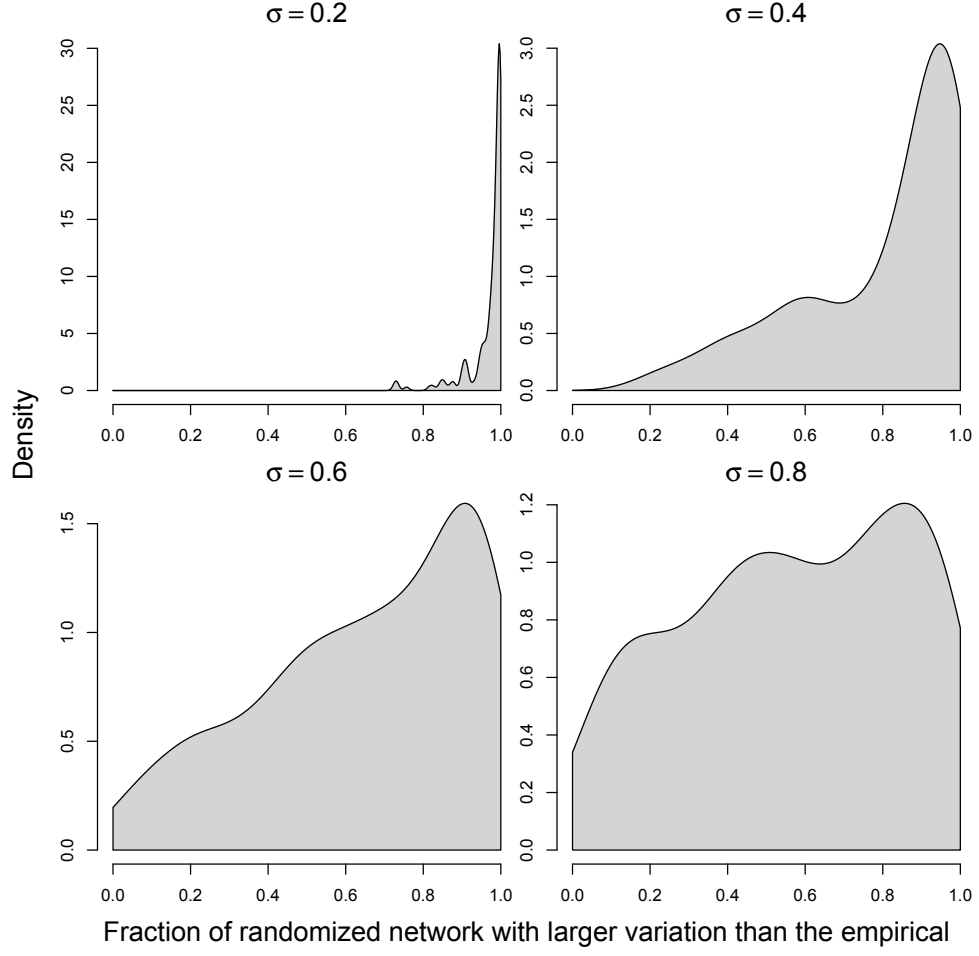


Figure S1: Observed and expected variations in the likelihood of persistence between summer and winter as function of variance  $\sigma$ . Histograms represent the fraction of expected persistence likelihood variations between randomized networks that are larger than the observed variation in the likelihood of persistence.

# Appendix S3 from S. Saavedra et al., “Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence”

## Mathematical derivation of likelihood of community persistence

Here we provide the mathematical derivation of the Equation 4 in the main text, which is used to estimate the size of the feasibility domain from the predator-prey model given by:

$$\frac{dC_i}{dt} = C_i \left( -m_i + \epsilon_i \sum_k \gamma_{ki} R_k \right) \quad (\text{S3a})$$

$$\frac{dR_k}{dt} = R_k \left( \alpha_k - R_k - \sum_i \gamma_{ki} C_i \right), \quad (\text{S3b})$$

where the variables  $C_i \geq 0$  and  $R_k \geq 0$  denote the biomass of predator (consumer)  $i$  and of prey (resource)  $k$ , respectively. The parameters are:  $m_i > 0$  the mortality rate of predator  $i$ ,  $\alpha_k > 0$  the intrinsic growth rate of prey  $k$ ,  $\epsilon_i = 0.1$  the standard conversion efficiency of predator  $i$  (Rossberg, 2013), and  $\gamma_{ki}$  is the trophic interaction strength between prey  $k$  and predator  $i$ . The elements  $\gamma_{ki}$  of the trophic interaction strength matrix are by definition the rate of the per capita effect of predator  $i$  on prey  $k$ . Recall that in our model we do not include intraguild predation because this is not observed in the data. Importantly, note that all parameters of the model are positive.



As demonstrated by Case (2000) and explained in our main text, for a large range of parameter values and assumptions, the dynamical system S3 converges to a globally stable equilibrium point  $(\mathbf{C}^*, \mathbf{R}^*)$ . The main assumptions behind that analytical result are two: that the number of prey is larger than the number of consumers, and that the matrix of trophic-interaction strength is full rank. The global stability of the equilibrium point is independent on the mortality rate  $m_i$  and intrinsic growth rate  $\alpha_k$  values.

However, the biomass at equilibrium  $(\mathbf{C}^*, \mathbf{R}^*)$  is a function of both the mortality and intrinsic growth rate values. Therefore, as explained in our main text, the remaining question is whether the dynamical system will converge into a positive equilibrium point (i.e.,  $C_i^* > 0$  and  $R_k^* > 0$ ). For this, we study the domain in the parameter space of mortality rate and intrinsic growth rate ( $m_i > 0$  and  $\alpha_k > 0$ ) leading to the existence of a positive equilibrium point ( $C_i^* > 0, R_k^* > 0$ ), and more importantly, how this domain is modulate by trophic-interaction strengths ( $\gamma_{ki}$ ).

The first step is to write the equations that define the positive equilibrium point ( $C_i^* > 0, R_k^*$ ). They are given by finding the no-trivial zero of the dynamical system S3. In a matrix form, these equations read as follow:

$$\mathbf{m} = \text{diag}(\epsilon) \boldsymbol{\gamma}^t \mathbf{R} \quad (\text{S4a})$$

$$\boldsymbol{\alpha} = \mathbf{R} + \boldsymbol{\gamma} \mathbf{C}, \quad (\text{S4b})$$

where  $\boldsymbol{\gamma}$  is the matrix of trophic-interaction strengths. These equations show that the set of mortality and growth rate values compatible with the existence of a positive equilibrium point have to be written as a linear combination of positive numbers. Therefore, mortality and growth rate need automatically to be positive, which act as an

ecological constraint. This set of mortality and growth rate values can be rewritten as

$$D_F = \{\alpha_i = x_i + \gamma_{i1}y_1 + \dots + \gamma_{iS_C}y_{S_C} \text{ and } m_i = \epsilon_i\gamma_{1i}x_1 + \dots + \epsilon_i\gamma_{S_Ri}x_{S_R} \mid \text{with } x_i > 0 \text{ and } y_i > 0\}. \quad (\text{S5})$$

The domain  $D_F$  is the so-called the feasibility domain. Note that this domain is a function of the trophic-interaction strength. Also, recall that this feasibility domain is never empty: it is always possible to choose values for  $m_i$  and for  $\alpha_k$  such that we obtain a positive solution ( $C_i^* > 0$  and  $R_k^* > 0$ ). For example, we can set  $m_i = \epsilon_i \sum_k \gamma_{ki}$  and  $\alpha_k = R_k + \sum_i \gamma_{ki}$ , and the corresponding stable positive equilibrium point is simply  $R_k = 1$  and  $C_i = 1$ . This simple example stresses the importance of not only looking at whether the system can reach a positive solution, but also at how large the feasibility domain is (how big the set of vectors leading to a positive stable solution is).

The second step is then to study the geometry of the feasibility domain defined by equation (S5). It is then useful to rewrite the equation defining the feasibility domain (equation (S5)) in a matrix form. For that we introduce the following matrix  $A$ , embedding all the interspecific interactions.

$$\mathbf{A} = \begin{bmatrix} \text{diag}(\boldsymbol{\epsilon})\boldsymbol{\gamma}^t & 0 \\ I & \boldsymbol{\gamma} \end{bmatrix} = \begin{bmatrix} \vdots & \vdots & & \vdots \\ \mathbf{v}_1 & \mathbf{v}_2 & \dots & \mathbf{v}_{S_R+S_C} \\ \vdots & \vdots & & \vdots \end{bmatrix}, \quad (\text{S6})$$

where  $I$  stands for the identity matrix. Moreover, each column of this matrix  $A$  corresponds to a column-vector  $\mathbf{v}_i$ . Now the feasibility domain can be rewritten as the set

of all positive linear combinations of the column-vector  $\mathbf{v}_i$ , i.e.,

$$\mathbf{A} = \begin{bmatrix} \mathbf{m} \\ \mathbf{\alpha} \end{bmatrix} = x_1 \mathbf{v}_1 + x_2 \mathbf{v}_2 + \cdots + x_{S_R+S_C} \mathbf{v}_{S_R+S_C}, \quad (\text{S7})$$

with,  $x_i > 0$ . Geometrically, such set is represented by an algebraic cone. For illustration purposes, Figure S1 gives an graphical representation of this cone in a subspace of three species. The three dotted green lines represent the three column-vectors of the matrix  $A$ ; which generate the cone. The green area represents the intersection of the cone with the unit simplex represented by the gray triangle.

Finally, we can compute the likelihood of community persistence by computing the area of the green section relative to the gray triangle (the unit simplex). This relative area is given by:

$$\Omega(\gamma) = \frac{\det(\mathbf{A})}{\prod_j (\sum_i A_{ij})}, \quad (\text{S8})$$

This equation has already been used by Svirezhev and Logofet (1983); Logofet (1993) in the case of a pure competition system. This formula can be interpreted in the following probabilistic way: it is the probability of sampling a vector of growth rate and mortality rates  $(\mathbf{m}, \mathbf{\alpha})$  that falls inside the cone of the feasibility domain. This follows the assumption of sampling uniformly and with a fixed sum. Importantly, note that we can use the formula (S8) only because all the elements of the matrix  $A$  are positive.

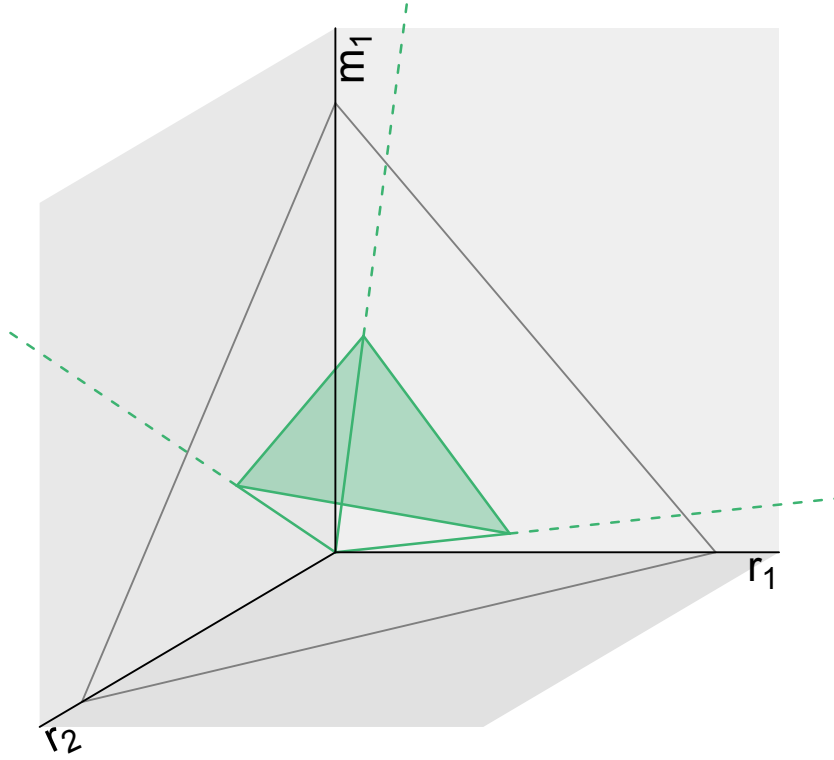


Figure S1: Geometric representation of the feasibility domain for a subset of three species. The feasibility domain is represented by an algebraic cone with its borders defined by the three green lines. The green lines are generated by the columns of the matrix  $A$  ( $\mathbf{v}_1$ ,  $\mathbf{v}_2$ ,  $\mathbf{v}_3$  of equation (S7)), which include all the interspecific interaction strengths. The green section represents the intersection of the feasibility cone with the unit simplex defined by the gray triangle. The area of the green section, relative to the unit simplex, gives the likelihood of community persistence and is computed by equation (S8)

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