

Why are some plant–pollinator networks more nested than others?

Chuliang Song¹  | Rudolf P. Rohr²  | Serguei Saavedra¹ 

¹Department of Civil and Environmental Engineering, MIT, Cambridge, MA, USA

²Department of Biology, Ecology and Evolution, University of Fribourg, Fribourg, Switzerland

Correspondence

Serguei Saavedra
Email: sersaa@mit.edu

Funding information

Funding to S.S. was provided by the MIT Research Committee Funds and the Mitsui Chair.

Handling Editor: Anna Eklöf

Abstract

1. Empirical studies have found that the mutualistic interactions forming the structure of plant–pollinator networks are typically more nested than expected by chance alone. Additionally, theoretical studies have shown a positive association between the nested structure of mutualistic networks and community persistence. Yet, it has been shown that some plant–pollinator networks may be more nested than others, raising the interesting question of which factors are responsible for such enhanced nested structure.
2. It has been argued that ordered network structures may increase the persistence of ecological communities under less predictable environments. This suggests that nested structures of plant–pollinator networks could be more advantageous under highly seasonal environments. While several studies have investigated the link between nestedness and various environmental variables, unfortunately, there has been no unified answer to validate these predictions. Here, we move from the problem of describing network structures to the problem of comparing network structures. We develop comparative statistics, and apply them to investigate the association between the nested structure of 59 plant–pollinator networks and the temperature seasonality present in their locations.
3. We demonstrate that higher levels of nestedness are associated with a higher temperature seasonality. We show that the previous lack of agreement came from an extended practice of using standardized measures of nestedness that cannot be compared across different networks.
4. Importantly, our observations complement theory showing that more nested network structures can increase the range of environmental conditions compatible with species coexistence in mutualistic systems, also known as structural stability. This increase in nestedness should be more advantageous and occur more often in locations subject to random environmental perturbations, which could be driven by highly changing or seasonal environments. This synthesis of theory and observations could prove relevant for a better understanding of the ecological processes driving the assembly and persistence of ecological communities.

KEYWORDS

changing environments, nestedness, network comparison, seasonality, structural stability, z-scores

1 | INTRODUCTION

Plant–pollinator networks are the synthesis of mutualistic interactions between flowering plants and their pollinators co-occurring in a given local site and time frame (Bascompte & Jordano, 2013). These networks are considered to have a structure more nested than expected by chance alone (Bascompte, Jordano, Melián, & Olesen, 2003). That is, if one compares the observed networks against random networks where the interactions have been arbitrarily shuffled, one typically observes an over-representation of shared mutualistic interactions between specialist (species with few interactions) and generalist species (species with many interactions). Traditionally, this nested structure refers to the network topology (i.e. the presence or absence of interactions). While quantitative measures of nestedness have been proposed (Almeida-Neto & Ulrich, 2011; Staniczenko, Kopp, & Allesina, 2013), their application to observed networks is still limited for two main reasons: theoretically it has been shown that the topology and the interaction strength of mutualistic networks play a separate role in shaping species persistence (Rohr, Saavedra, & Bascompte, 2014; Saavedra, Rohr, Dakos, & Bascompte, 2013), and the frequency of interactions is not enough to parameterize interaction strengths (Schupp, Jordano, & Gómez, 2017). These results have generated a rich research agenda on understanding the factors modulating the nested structure (topology) of mutualistic networks in general (Bascompte & Jordano, 2013).

Importantly, seminal work has predicted that more *ordered* network structures (as opposed to random network structures) should be found in less predictable environments (Levins, 1968; Margalef, 1968; May, 1975; Odum, 1969). The rationale is that under less predictable environments, species may enhance their tolerance to external disturbances through well-structured communities. In this line, theoretical work has shown that a nested structure in plant–pollinator networks can enhance species coexistence by minimizing species competition, and by increasing the range of intrinsic conditions leading to positive species abundances (Bastolla et al., 2009; Rohr et al., 2014; Saavedra, Rohr, Olesen, & Bascompte, 2016; Saavedra & Stouffer, 2013). For instance, recent work has shown that by keeping the same level of mean interaction strength, the more nested a structure in a mutualistic system, the more tolerant the community would be to random perturbations to intrinsic growth rates (Rohr et al., 2014; Saavedra, Rohr, Olesen, et al., 2016). This tolerance is also known as the structural stability of community persistence (Rohr et al., 2014; Saavedra et al., 2017). Thus, it can also be predicted that nested network structures should be more advantageous and occur more often in locations subject to highly changing or seasonal environments.

Several studies have pointed to different environmental and anthropogenic factors as modulators of the nested pattern of plant–pollinator networks; however, little agreement has been found on specific effects (Dalsgaard et al., 2013; Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015; Takemoto & Kajihara, 2016; Takemoto, Kanamaru, & Feng, 2014; Trøjelsgaard & Olesen, 2013; Welti & Joern, 2015). For example, looking at the association between nestedness and temperature seasonality, different studies have found both a negative and a positive relationship (Sebastián-González et al., 2015;

Takemoto & Kajihara, 2016). Undoubtedly, knowing the reasons for these contrasting findings can allow us to increase our understanding about the processes modulating the nested structure and potentially the persistence of ecological communities. One candidate explanation for these differences is the statistical analysis itself, in which case the effect of predictor variables could be difficult to reconcile as many different correlated environmental and ecological variables are continuously added into multivariate regression analyses (Legendre & Legendre, 2012). A more fundamental problem, however, could be a misuse of the statistical metrics employed to compare across networks. In such case, this problem could be corrected and applied across studies. In this manuscript, to test the predictions above, we review comparative metrics of nestedness, signal important misuses, and provide a methodology to correct them. Then, we apply the new proposed metrics to observed plant–pollinator networks and environmental data to investigate whether more nested structures are found in more seasonal locations.

2 | MATERIALS AND METHODS

In this section, first we will define how we calculate nestedness. Then we will show how this measure has been used to compare nestedness across networks. Then we will present the limitations of current comparative approaches. Then we will develop a new statistic to correct for these limitations. Finally we will show how we investigate the link between nestedness and temperature seasonality.

To calculate nestedness, we used a standard measure known as NODF (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). In fact, several metrics of nestedness have been proposed since it was first introduced in the field of island biogeography by Atmar and Patterson (1993) and then applied to mutualistic networks (Bascompte et al., 2003). Today, one of the most intuitive measures of nestedness is NODF, which has shown to be a consistent metric based on two basic properties derived from the original concept of nestedness: species can be arranged in decreasing order according to their number of mutualistic partners, and the mutualistic partners of species with few interactions are typically shared with species with more interactions (Almeida-Neto et al., 2008). Note that other measures of nestedness are highly correlated to NODF (Saavedra et al., 2013; Ulrich, Almeida-Neto, & Gotelli, 2009).

However, NODF (as other measures of network structure) is not exempt from having strong correlations with other network descriptors (Ulrich et al., 2009). For instance, using a set of 59 plant–pollinator networks extracted from the public repository web-of-life.es, Figure 1a,b show, respectively, the strong positive and negative association of NODF with connectance and number of species in the network ($r = .86$ and $-.71$, Pearson correlation). Note that connectance is defined as the fraction of observed interactions relative to the maximum possible, while the number of species is calculated by the geometric mean of plants and pollinators. These relationships become even more entangled as connectance and the number of species are also highly correlated ($r = -.81$, Pearson correlation). Overall, these strong correlations

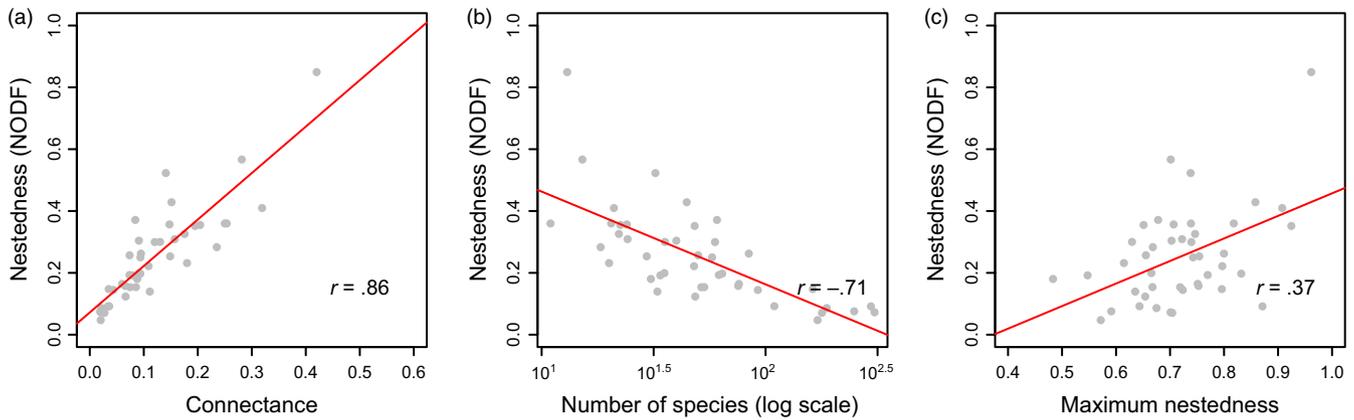


FIGURE 1 Association of nestedness with other network descriptors and constraints. For 59 observed plant–pollinator networks, (a) and (b) show the positive and negative association of nestedness (NODF) with connectance and number of species (log of geometric mean of plants and pollinators) respectively. Results are qualitatively the same if the number of species is calculated by the log of the sum of plants and pollinators. (c) It illustrates the positive association between nestedness (NODF) and the maximum value of nestedness that can be reached in the corresponding network (calculated using a greedy algorithm). Each point corresponds to one of the 59 networks. The red lines correspond to the linear regression (intended to guide the eye), and r corresponds to the Pearson correlation (all correlations were significant at the 5% confidence level) [Colour figure can be viewed at wileyonlinelibrary.com]

imply that the raw values of NODF cannot be used to compare nestedness across different networks (Ulrich et al., 2009). Note that these 59 plant–pollinator networks correspond to the aggregated observations of pollinator visitations over different periods of time, meaning that the structures and therefore the correlations must be taken with caution (Trøjelsgaard & Olesen, 2016). Yet, it has been shown that plant–pollinator networks can display consistent structures even at the daily level (Saavedra, Rohr, Olesen, et al., 2016).

Additionally, measures such as NODF, are constructed between some boundary values. For instance, $NODF \in [0, 1]$, where the higher the value, the higher the nested structure of the network. Nevertheless, because of the constraints imposed by the number of species and interactions, the realized minimum and maximum values for these measures can be different from those initially expected (Rohr et al., 2014; Saavedra, Rohr, Olesen, et al., 2016). Using NODF and without assuming any additional constraints other than the number of species and interactions, by construction, the minimum values are almost zero for all the observed 59 plant–pollinator networks (Almeida-Neto et al., 2008). However, the maximum values can be significantly less than one (Rohr et al., 2014; Saavedra, Rohr, Olesen, et al., 2016). These maximum values can be found using a greedy algorithm (Cormen, Leiserson, Rivest, & Stein, 1990). Specifically, starting with a minimum requirement of a plant–pollinator network (each pollinator interacts with at least one plant), we added a new interaction by choosing the one that would give the highest NODF out of all combinations. We iterated this process until the number of observed interactions is reached (R-code provided in Song, Rohr, & Saavedra, 2017). In our dataset, maximum values range in $[0.48, 0.96]$ and are positively correlated ($r = .37$, Pearson correlation) with the observed value of NODF (see Figure 1c). This further reveals that NODF values need to be normalized by their realized maximum values to be used as a fair comparison measure of nestedness across networks.

To correct for some of the problems mentioned above, studies have been comparing nestedness across networks using z-scores (Dalsgaard et al., 2013; Gilarranz, Sabatino, Aizen, & Bascompte, 2015; James, Pitchford, & Plank, 2013; Nielsen & Bascompte, 2007; Sebastián-González et al., 2015; Takemoto & Kajihara, 2016; Takemoto et al., 2014; Trøjelsgaard & Olesen, 2013; Welti & Joern, 2015). These standardized values are defined as $z = (NODF - \mu)/\sigma$, where μ and σ are the mean and SD of the distribution of NODF values (or any other measure of nestedness) generated by a chosen null model. The most common null models are known as the equiprobable, probabilistic and fixed models (Bascompte et al., 2003; Ulrich et al., 2009). The equiprobable model assigns the same probability to each potential interaction in the network. The probabilistic model assigns a probability to each potential interaction proportional to the number of observed interactions between mutualistic partners. Note that the equiprobable and probabilistic models provide almost identical results (Ulrich et al., 2009). The fixed model randomly shuffles the interactions while preserving the observed number of mutualistic partners of each species. In general, when comparing two networks, the one with the higher z-score is considered to be more nested (James et al., 2013). However, z-scores should not be used for comparison purposes for two main reasons: one statistical and one related to inconsistency problems (Gelman & Stern, 2006; Johnson, 1999).

The statistical problem has to do with the fact that the z-score strongly depends on network size. Recall that the z-score is computed by dividing the difference between the observed level of nestedness (NODF) and the expected level (under the null model) by the SD of the null model. Nevertheless, the SD decreases as the inverse of the square root of the number of species (see Figure 2a). In fact, this SD has the same scaling property as a standard error in statistics (Zar, 2010). Consequentially, rejecting the null hypothesis or having a high z-score becomes easier to achieve under large networks.

To illustrate this situation, for different numbers of species, we randomly generated 1,000 networks using the equiprobable model (other

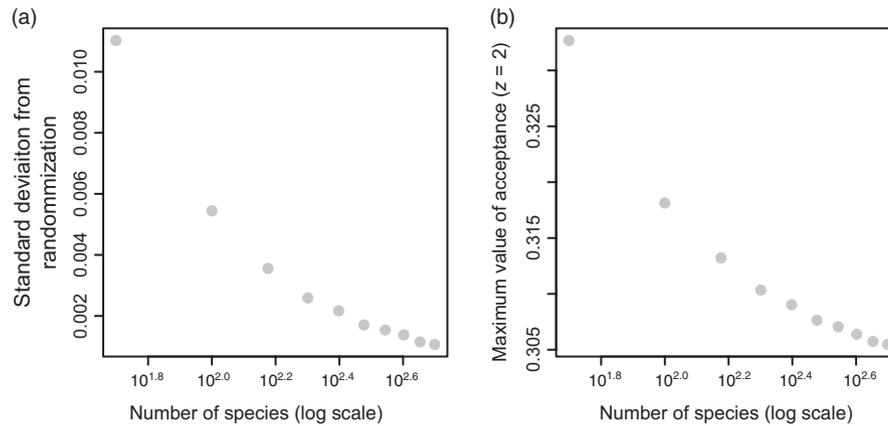


FIGURE 2 Dependency of null models on data points. Calculating NODF on randomly generated matrices (using the equiprobable model), the figure shows the SD (σ) and the standard maximum value of acceptance of the null hypothesis ($\mu + 2\sigma$, equivalent to z -score = 2) as a function of the number of species on a log scale (data points). Each point is generated by sampling random interactions matrices (1's and 0's) with a fixed connectance of 0.3. Note that the number of species modulates the SD (a), which in turn, modulates proportionally the z -score (b)

null models lead to the same conclusions), calculated their NODF values, and computed their SD (σ) and standard region of acceptance ($\mu + 2\sigma$, equivalent to $z = 2$). These random networks had a fixed connectance of 0.3 and vary in size from 50 to 350 species (other parameter values lead to the same conclusion). Figure 2 shows that the SD of these networks decreases as a nonlinear function of the number of species, consequently making the region of acceptance proportionally smaller. This implies that raw values of NODF will more likely fall outside the region of acceptance (larger z -scores) in large networks. Thus, we cannot fairly conclude that a network with a z -score of 3 is more nested than a smaller network with a z -score of 2 (Gelman & Stern, 2006; Johnson, 1999).

The problem related to inconsistency relates to the fact that even if we grant that z -scores from different networks may be compared, these z -scores are inconsistent across different levels of connectance and number of species. This statement can be derived from the fact that a z -score is equivalent to a p -value in statistics, which is only valid for a particular data and model (Gelman & Stern, 2006; Johnson, 1999; Legendre & Legendre, 2012). That is, unless z -scores are generated from networks with the same descriptors (connectance, size, etc.), the probability distribution of values generated by any null model would be different. This inconsistency problem limits the capacity of z -scores to detect structural similarities between different networks, even when these networks are generated with the same mechanism.

To illustrate the problem of z -scores related to inconsistency, we constructed 1,000 random networks using the equiprobable model (with different connectance and sizes), calculated their NODF values, computed the expected z -score (using the probabilistic and fixed models), and checked whether the expected z -scores changed across networks with different sizes and connectance. The randomizations used to calculate the expected z -scores are done following the equiprobable model using upper triangular matrices (all interactions are zero below the main diagonal). This is done in order to increase the accuracy of the expectations by decreasing the sampling space (results are qualitatively the same without this restriction). This was

repeated for different sizes (between 20 and 60 species) and different values of connectance (between 0.1 and 0.4). Because all networks are constructed in the exact same unstructured way (i.e. following the equiprobable model), there is no reason to expect that an average network generated with given parameters should be more or less nested than an average network generated with other parameters. Any potential difference should be simply a consequence of changing connectance and size. While it is believed that z -scores should control for these potential differences, Figure 3 clearly shows that both the probabilistic and fixed models continue to display significant differences in the expected z -scores as function of connectance and size. This confirms that z -scores are not a consistent statistical measure of nestedness across networks.

To compare nestedness across networks and be able to investigate its association with temperature seasonality, we need to develop nestedness statistics with independent properties from maximum nestedness, network size and connectance. To do this, we can properly normalize nestedness values and combine them with network descriptors (Legendre & Legendre, 2012; Zar, 2010). Because we know that the maximum value of nestedness is not the same for every network (see Figure 1c), a good candidate for normalization is the value of nestedness relative to its maximum possible value, i.e. $NODF_n = NODF / \max(NODF)$. Additionally, as we know that connectance and size are strong modifiers of nestedness, we can combine these network descriptors with our normalized value of nestedness to control for these effects. Here, we used the simplest multiplicative interaction given by $NODF_c = NODF_n / (C \cdot \log(S))$, where C and $\log(S)$ are the connectance and the log of the geometric mean of plants and pollinators in the network (results are qualitatively the same if using the log of the sum of plants and animals). Note that we use $\log(S)$ instead of the raw number of species because only with $\log(S)$, $NODF_c$ remains independent from network size (see Figure S1).

To test the combined nestedness statistic, we repeated the consistency analysis above, but we replaced the z -scores with $NODF_c$. Figure 3 confirms that the combined nestedness statistic is in fact

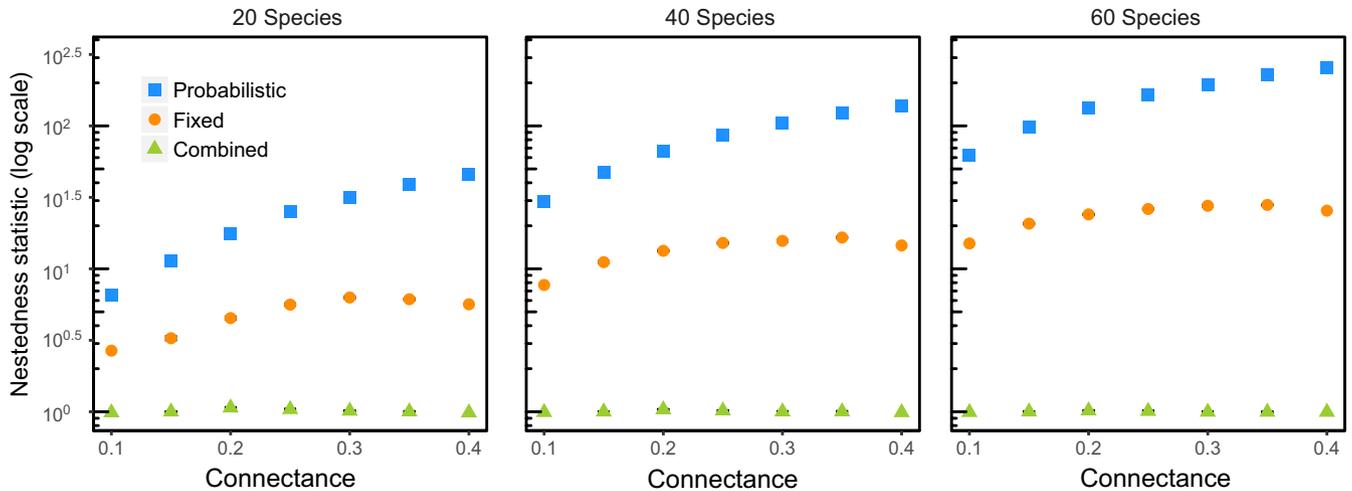


FIGURE 3 Comparing nestedness across identically generated networks. For ensembles of 1,000 randomly generated networks with the same unstructured mechanism (using the equiprobable model), the figure shows the average nestedness statistic (on a log scale for visualization purposes) as function of different values of connectance [0.1; 0.4] (x-axis) and community size (20, 40 and 60 species). The blue squares, orange circles and green triangles correspond to the nestedness statistic using the z-score with probabilistic model, z-score with fixed model and the combined nestedness respectively. Note that only the combined nestedness statistic displays a more consistent measure across network dimensions. All error bars around the average value were negligible. Because the nestedness statistic for the fixed model is negative, we used $\log(z\text{-score} + 10)$ for its visualization [Colour figure can be viewed at wileyonlinelibrary.com]

consistent across network size and connectance. This shows that a combined statistic can be a more reliable measure than z-scores to compare nestedness across networks. Importantly, the consistency of this combined statistic allows our investigation of the potential association between nestedness and temperature seasonality.

Finally, to test the hypothesis that nestedness should increase under changing environmental conditions, we investigated the association between the combined nestedness statistic (NODF_c) and the level of temperature seasonality (variance of daily temperature) in different locations around the world. The latitude and longitude of the observed plant–pollinator networks were obtained from the public repository *web-of-life.es*. Environmental data were obtained from the public repository *WorldClim* (version 1.4, release 3, resolution 2.5 min). Using these repositories, we gathered environmental data for 43 out of the 59 networks. We did not find information about the other 16 networks (network and temperature data are provided in Song et al., 2017). To study the direct relationship between the combined nestedness statistic and temperature seasonality, first we used a simple correlation analysis. Because it is not expected that only one factor (e.g. temperature seasonality) should perfectly explain the structure of ecological networks (Trøjelsgaard & Olesen, 2016), we also used a standard principal component analysis (PCA; Legendre & Legendre, 2012). This approach allowed us to project the multidimensional variation of the dataset into fewer dimensions (principal components). We used the combined nestedness statistic, $\log(S)$, connectance and temperature seasonality as variables in our PCA. Thus, the PCA illustrates the correlations between these variables and how they explain the variances in the data. Additionally, we compared the correlation and PCA results against the results from standardized values of nestedness (z-scores).

3 | RESULTS

Focusing on the simple correlations between the nestedness statistics and temperature seasonality, Figure 4a,b shows that the z-scores derived from the probabilistic and the fixed models have nearly a null correlation ($r = .02$ and $-.07$, Pearson correlation). In contrast, the figure (Figure 4c) shows that the combined nestedness statistic has a positive correlation with temperature seasonality ($r = .27$, Pearson correlation). Note that both the outliers and the low correlation warn caution on interpreting this result. For example, removing points larger than two *SDs* away from the mean on both variables makes this positive correlation non-significant.

To further investigate these relationships above, we shift our focus to the PCA. Figure 5 shows the two principal components derived from the four variables: nestedness statistic (z-scores and combined nestedness), number of species (log of the geometric mean of plants and pollinators), connectance and temperature seasonality. The two components accounted for c. 75% of the variance in the data. The figure (Figure 5a,b) shows that using z-scores, the nestedness statistic is highly correlated with size and connectance for the probabilistic and fixed models respectively. This association can be observed by noticing the same direction of their corresponding vectors. Not surprisingly, both z-scores were poorly correlated with temperature seasonality, i.e. the vectors of the nestedness statistic and temperature seasonality were positively correlated on one component but negatively on the other. These results confirm previous work showing that z-scores derived from different null models (probabilistic and fixed models) can generate different patterns and no unified answers (Sebastián-González et al., 2015; Takemoto & Kajihara, 2016).

Importantly, Figure 5c shows that the combined nestedness statistic has a strong correlation with temperature seasonality. That is, the vectors of nestedness and seasonality show similar directions on both components. Note that combined nestedness statistic and temperature seasonality are nearly orthogonal to connectance and size. These qualitative results did not change by removing the outliers defined above from Figure 4c (see Figure S2). These results then support the hypothesis that more nested structures of plant–pollinator networks (when accounting for the intrinsic effects of connectance and community size) should be found in more seasonal or environmentally less predictable locations.

4 | DISCUSSION

A central line of research on the study of mutualistic communities has been to understand the extent to which the structure of plant–pollinator networks can modulate the likelihood of species persistence (Bascompte & Jordano, 2013). Theoretically, it has been shown that the nested structure of mutualistic networks can have important consequences for biodiversity maintenance (Bastolla et al., 2009; Rohr et al., 2014; Saavedra et al., 2013; Saavedra, Rohr, Olesen, et al., 2016). Thus, studies have been investigating which ecological and environmental conditions could be associated with an increase

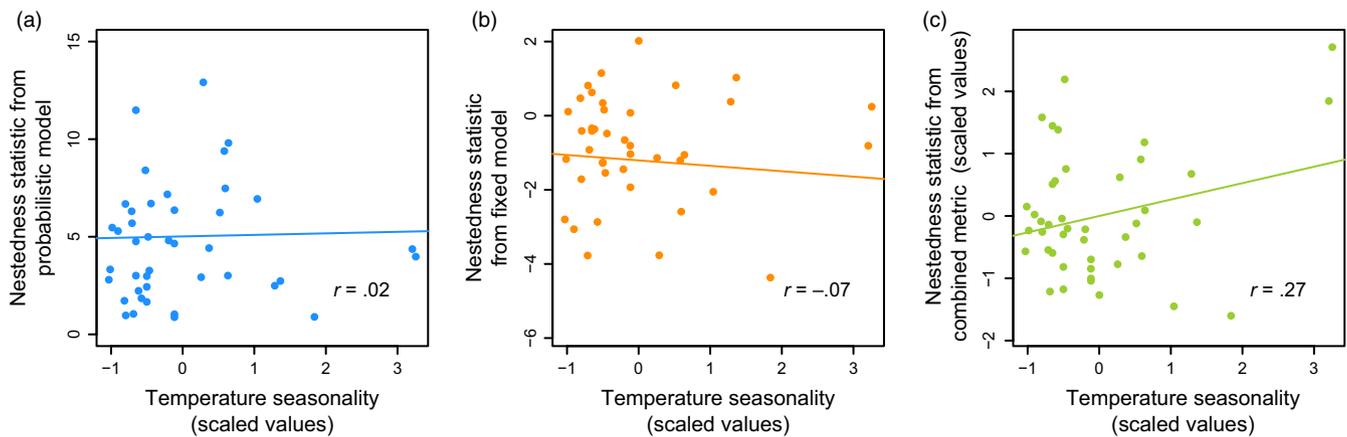


FIGURE 4 Association of temperature seasonality with nestedness statistics. For 43 observed plant–pollinator networks (with environmental data), (a–c) illustrate the association of the scaled temperature seasonality (x-axis) with the nestedness statistic derived from the probabilistic model, the fixed model and the combined nestedness (scaled values) respectively. Each point corresponds to one of the 43 networks. The solid lines correspond to the linear regression (intended to guide the eye), and r corresponds to the Pearson correlation (only the correlation with combined nestedness statistic was significant at the 5% confidence level) [Colour figure can be viewed at wileyonlinelibrary.com]

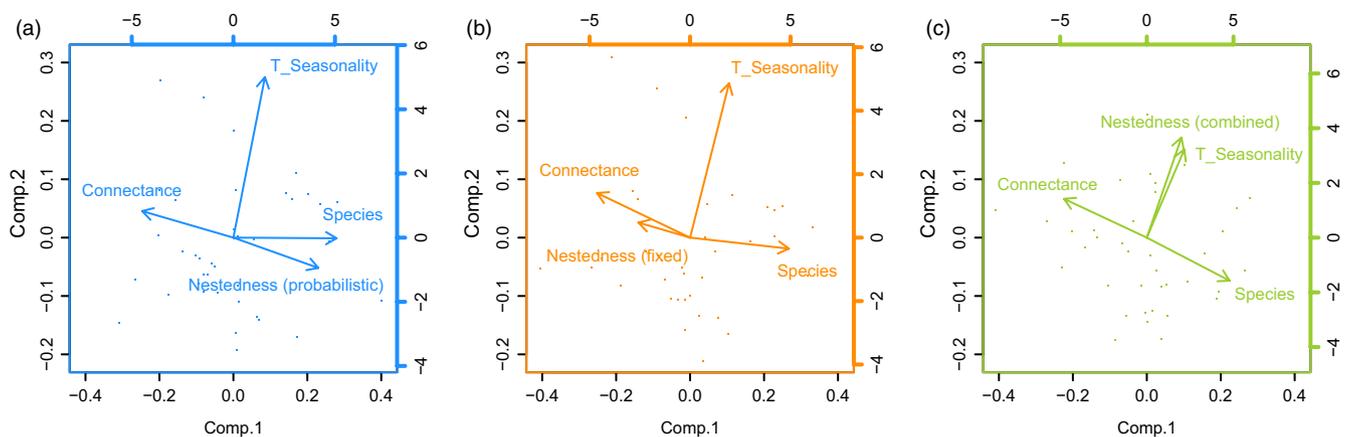


FIGURE 5 Identifying the direction of change between nestedness and temperature seasonality. Using a principal component analysis (Legendre & Legendre, 2012), the figure shows the two principal components for the four variables investigated: number of species (log of the geometric mean of plants and pollinators), connectance, nestedness statistic and temperature seasonality. The arrows correspond to the four associated eigenvectors, and each small dot corresponds to one of the 43 observed plant–pollinator networks (with environmental data). Note that the bottom and left axes correspond to the scaled values, whereas the top and right axes correspond to the vector loadings. (a–c) It correspond to the nestedness statistic using the z-score with probabilistic model, z-score with fixed model, and the combined nestedness respectively. Note that only the combined nestedness statistic (c) displays a strong overlap with temperature seasonality, and both are almost orthogonal to connectance and number of species [Colour figure can be viewed at wileyonlinelibrary.com]

of these nested structures in mutualistic networks (Dalsgaard et al., 2013; Gilarranz et al., 2015; Nielsen & Bascompte, 2007; Sebastián-González et al., 2015; Takemoto & Kajihara, 2016; Takemoto et al., 2014; Trøjelsgaard & Olesen, 2013; Welty & Joern, 2015).

Unfortunately, there has not been a unified answer regarding the environmental modulators of nestedness. However, as we have shown in this manuscript, the comparative approach (*z*-scores) used by previous studies has important statistical limitations and problems related to inconsistency. *Z*-scores provide no certainty that one network is more nested than other, they simply provide information of whether networks are different or not from a null model (Gelman & Stern, 2006; Johnson, 1999). Therefore, *z*-scores can be used to reveal patterns relative to null expectations, but they should not be used to compare nestedness across different networks, or to analyse the association of nestedness with community persistence and other environmental factors. Note that this concern is not unique to nestedness in plant–pollinator networks, these standardized values have been used extensively to compare different structural properties across ecological networks.

To address this problem, we have proposed to use a normalized and combined nestedness statistic to provide an independent relationship between nestedness and other network descriptors, especially network size and connectance. This combined statistic takes into account the realized maximum values of nestedness in a network, and combines the key descriptors of connectance and size as nonlinear penalties for nestedness. In fact, our PCA analysis has shown that this combined statistic is almost orthogonal to connectance and size, making it a good candidate for comparison purposes (Legendre & Legendre, 2012; Zar, 2010). Yet, the reader is encouraged to find other comparative metrics appropriate for their own research questions taking into account the statistical and inconsistency problems we have previously discussed. Note that the combined nestedness statistic must not be interpreted in the same way as raw nestedness. It also does not answer whether a network is significantly nested or not. This measure only gives the level of nestedness relative to the interaction of other network descriptors and constraints, which only provides a fair statistical ground for comparison purposes (Legendre & Legendre, 2012).

Why, then, are some plant–pollinator networks more nested than others? Recent theoretical studies have pointed out that nestedness can modulate the structural stability of the persistence of plant–pollinator communities (Rohr et al., 2014; Saavedra, Rohr, Olesen, et al., 2016). That is, under the same levels of mutualistic strength, nestedness can theoretically increase the range of environmental conditions compatible with species coexistence. This effect could be particularly advantageous when communities are subject to highly changing (less predictable) environments (Levins, 1968; Margalef, 1968; May, 1975; Odum, 1969). However, under low environmental stochasticity (Rohr et al., 2016; Saavedra, Rohr, Fortuna, Selva, & Bascompte, 2016; Saavedra, Rohr, Gilarranz, & Bascompte, 2014), increasing nestedness may be costly for some species in the community (Saavedra, Stouffer, Uzzi, & Bascompte, 2011). Thus, we should expect to see more nested structures under unpredictable environments leading to random environmental perturbations.

Using a comparable measure of nestedness across networks, our findings support the hypothesis above stating that nestedness should increase under more seasonal or changing environments. Note that this finding does not rely on the fact that a plant–pollinator network can be more or less nested than expected by chance. It only provides information about the conditions under which nested structures should be more advantageous and occur more often. One should not always make equivalent the difficulty of detecting a structural pattern in a network to the dynamical implications of such structure (e.g. Strona & Veech, 2015).

We have used temperature variance as a proxy for changing environments; however, future work could explore the extent to which other variables can provide a better proxy for how environments are randomly changing in relation to the community under investigation. We would also like to encourage others to further test these ideas on data properly designed and collected for this type of analysis (Trøjelsgaard & Olesen, 2016). We have used data whose level of confidence have not been assessed, sampling protocols can be quite different, interactions represent the aggregation of different observation periods, and constituent species can be biased towards particular groups. Therefore, before claiming any general results across networks, one would need to homogenize the use of network data to properly handle any case of outliers. We believe that combining appropriate comparative metrics, data, and hypotheses can lead to a rigorous synthesis between theory and observations that is relevant for a better understanding of the ecological processes driving the assembly and persistence of ecological communities.

ACKNOWLEDGEMENTS

We thank Nick Simmons for his help in compiling the data. We also thank two anonymous reviewers for the highly constructive comments that led to the improvement of this work. Funding to S.S. was provided by the MIT Research Committee Funds and the Mitsui Chair. The authors declare no competing financial interests.

AUTHORS' CONTRIBUTIONS

S.S. and R.P.R. designed the study; C.S. performed the analysis; S.S. supervised the study; and S.S. wrote a first version of the manuscript. All authors contributed with significant revisions to the manuscript.

DATA ACCESSIBILITY

The data and R-code supporting the results are archived in Dryad Digital Repository <https://doi.org/10.5061/dryad.dv1gq> (Song et al., 2017).

ORCID

Chuliang Song  <http://orcid.org/0000-0001-7490-8626>

Rudolf P. Rohr  <http://orcid.org/0000-0002-6440-2696>

Serguei Saavedra  <http://orcid.org/0000-0003-1768-363X>

REFERENCES

- Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. *Oikos*, *117*, 1227–1239.
- Almeida-Neto, M., & Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software*, *26*, 173–178.
- Atmar, W., & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, *96*, 373–382.
- Bascompte, J., & Jordano, P. (2013). *Mutualistic networks*. Princeton, NJ: Princeton University Press.
- Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 9383–9387.
- Bastolla, U., Fortuna, M. A., Pascual-Garca, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, *458*, 1018–1020.
- Cormen, T. H., Leiserson, C. E., Rivest, R. L., & Stein, C. (1990). *Introduction to algorithms*. Cambridge, MA: MIT Press.
- Dalsgaard, B., Trøjelsgaard, K., González, A. M. M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., ... Olesen, J. M. (2013). Historical climate-change in uences modularity and nestedness of pollination networks. *Ecography (Cop.)*, *36*, 1331–1340.
- Gelman, A., & Stern, H. (2006). The difference between “significant” and “not significant” is not itself statistically significant. *The American Statistician*, *60*, 328–331.
- Gilarranz, L. J., Sabatino, M., Aizen, M. A., & Bascompte, J. (2015). Hot spots of mutualistic networks. *Jouyrnal of Animal Ecology*, *84*, 407–413.
- James, A., Pitchford, J. W., & Plank, M. J. (2013). James et al. reply. *Nature*, *500*, E2–E3.
- Johnson, D. H. (1999). The insignificance of statistical significance testing. *The Journal of Wildlife Management*, *63*, 763–772.
- Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd ed.). Amsterdam, the Netherlands: Elsevier.
- Levins, R. (1968). *Evolution in changing environments: Some theoretical explorations*. Princeton, NJ: Princeton University Press.
- Margalef, R. (1968). *Perspectives in ecological theory*. Chicago, IL: University of Chicago Press.
- May, R. M. (1975). Stability in ecosystems: Some comments. In W. H. van Dobben & R. H. Lowe-McConnell (Eds.), *Unifying concepts in ecology* (pp. 161–168). New York, NY: Springer.
- Nielsen, A. & Bascompte, J. (2007). Ecological networks, nestedness and sampling effort. *Journal of Ecology*, *95*, 1134–1141.
- Odum, E. P. (1969). The strategy of ecosystem development. *Science*, *164*, 262–270.
- Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, *345*, 1253497.
- Rohr, R. P., Saavedra, S., Peralta, G., Frost, C. M., Bersier, L.-F., Bascompte, J., & Tylianakis, J. M. (2016). Persist or produce: A community trade-off tuned by species evenness. *The American Naturalist*, *188*, 411–422.
- Saavedra, S., Rohr, R. P., Bascompte, J., Godoy, O., Kraft, N. J. B., & Levine, J. M. (2017). A structural approach for understanding multispecies coexistence. *Ecological Monographs*, *87*, 470–486.
- Saavedra, S., Rohr, R. P., Dakos, V., & Bascompte, J. (2013). Estimating the tolerance of species to the effects of global environmental change. *Nature Communications*, *4*, 2350.
- Saavedra, S., Rohr, R. P., Fortuna, M. A., Selva, N., & Bascompte, J. (2016). Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. *Ecology*, *97*, 865–873.
- Saavedra, S., Rohr, R. P., Gilarranz, L. J., & Bascompte, J. (2014). How structurally stable are global socioeconomic systems? *Journal of The Royal Society Interface*, *11*, 20140693.
- Saavedra, S., Rohr, R. P., Olesen, J. M., & Bascompte, J. (2016). Nested species interactions promote feasibility over stability during the assembly of a pollinator community. *Ecology and Evolution*, *6*, 997–1007.
- Saavedra, S., & Stouffer, D. B. (2013). “Disentangling nestedness” disentangled. *Nature*, *500*, E1–E2.
- Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, *478*, 233–235.
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2017). A general framework for effectiveness concepts in mutualisms. *Ecology Letters*, *20*, 577–590.
- Sebastián-González, E., Dalsgaard, B., Sandel, B., & Guimarães, P. R. (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global Ecology Biogeography*, *24*, 293–303.
- Song, C., Rohr, R. P., & Saavedra, S. (2017). Data from: Why are some plant-pollinator networks more nested than others? *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.dv1gq>
- Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature Communications*, *4*, 1391.
- Strona, G., & Veech, J. A. (2015). A new measure of ecological network structure based on node overlap and segregation. *Methods in Ecology and Evolution*, *6*, 907915.
- Takemoto, K., & Kajihara, K. (2016). Human impacts and climate change in uence nestedness and modularity in food-web and mutualistic networks. *PLoS ONE*, *11*, e0157929.
- Takemoto, K., Kanamaru, S., & Feng, W. (2014). Climatic seasonality may affect ecological network structure: Food webs and mutualistic networks. *Biosystems*, *121*, 29–37.
- Trøjelsgaard, K., & Olesen, J. M. (2013). Macroecology of pollination networks. *Global Ecology Biogeography*, *22*, 149–162.
- Trøjelsgaard, K., & Olesen, J. M. (2016). Ecological networks in motion: Micro- and macroscopic variability across scales. *Functional Ecology*, *30*, 1926–1935.
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, *118*, 3–17.
- Welti, E., & Joern, A. (2015). Structure of trophic and mutualistic networks across broad environmental gradients. *Ecology Evolution*, *5*, 326–334.
- Zar, J. H., 2010. *Biostatistical analysis* (5th ed.). Hoboken, NJ: Pearson.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Song C, Rohr RP, Saavedra S. Why are some plant-pollinator networks more nested than others? *J Anim Ecol*. 2017;1–8. <https://doi.org/10.1111/1365-2656.12749>