Structural changes within trophic levels are constrained by within-family assembly rules at lower trophic levels

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Abstract

Historical contingency broadly refers to the proposition that even random historical events can constrain the ecological and evolutionary pathways of organisms and that of entire communities. Focusing on communities, these pathways can be reflected into specific structural changes within and across trophic levels – how species interact with and affect each other – which has important consequences for species coexistence. Using the registry of the last 2000 years of plant introductions and their novel herbivores encountered in Central Europe, we find that the order of arrival of closely related (but not of distantly related) plant species constrained the structural changes within the trophic level formed by herbivore species across the observation period. Because it is difficult for field and lab experiments to be conducted over hundreds of years to record and replay the assembly history of a community, our study provides an alternative to understand how structural changes have occurred across extensive periods of time.

Keywords

Community assembly, ecological networks, historical contingency, species coexistence, structural stability.

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INTRODUCTION

In 1989, Stephen J. Gould posed the thought experiment of whether evolutionary history would take a very different route than the one we know today if we could rewind the tape of life and replay it again (Gould 1989). While historical events are difficult to reconstruct and replay over long periods of time, it has been shown that it may be possible to investigate the assembly rules shaping the biodiversity that we observe in nature (Thompson 1917; Fox 1987; Alberch 1989). Historical contingency broadly refers to the proposition that even random historical events (such as abiotic and biotic events) can constrain the ecological and evolutionary pathways of organisms and that of entire ecological communities (Fukami 2015). In an ecological context, these pathways can be reflected into specific structural changes within and across trophic levels, which are defined by how species interact with and affect each other (Odum 1969; Dormann *et al.* 2017; Godoy *et al.* 2018). This structure, which is summarised by the interaction matrix, has key implications for species coexistence (Case 2000; Saavedra *et al.* 2017b), and is highly dependent on the order and timing of species arrivals to the community (Diamond 1975; Chase 2003; Morin 2011). While assembly processes and their effects are typically investigated within a focal trophic level, numerous studies have shown that these effects can also impact the composition of species across different trophic levels (Drake 1991; Olito & Fukami 2009; Price & Morin 2004; Fukami 2015; Gomes *et al.* 2017). Yet, it remains unclear which are the main historical factors explaining the structural changes that we observe across trophic levels over time.

To shed new light onto the questions above, we study the order of arrival within the trophic level formed by plant species and its effect on the structure of the herbivore trophic level feeding on these plants. We study the structure of the herbivore trophic level by looking at how the competition matrix among herbivores (formed by shared plants) modulates the range of environmental conditions compatible with the persistence of the herbivore community – a measure that is typically called the structural stability of community persistence (Saavedra *et al.* 2017a, b). Because it is difficult for field and lab experiments to be conducted over extensive periods of time in order to record the assembly history of a community (Fukami & Morin 2003; Chase 2010; Leopold *et al.* 2017), we investigate historical events using the registry of the last 2000 years of plant introductions to Central Europe and the existing native herbivore communities in that region. These data allow us to answer the two following questions: Are there non-trivial structural changes within the herbivore trophic level formed by herbivore species competing for (sharing) plant hosts? How does the order of plant arrivals within and across families constrain structural changes within the herbivore trophic level?

METHODS

Observational data

We based our analysis on a plant–herbivore interaction matrix from the German State of Baden-Württemberg (35 751 km^2) in Central Europe (Altermatt & Pearse 2011; Pearse &

Altermatt 2013a, b, 2015). In a collaborative long-term effort (Ebert, 1991-2005), herbivory observations of > 2.342 million larval individuals of 759 Macrolepidopteran (i.e. butterflies and moths) species were recorded feeding on a total of 684 vascular plant species. All observations refer to interactions which have been observed under natural conditions in Baden-Württemberg since the beginning of the 20th century (Altermatt & Pearse 2011), possibly making it one of the most complete large plant–insect interaction data sets [see Pearse & Altermatt (2015) for tests of completeness and robustness].

In our data, all Macrolepidopterans and 501 vascular plants are native to Baden-Württemberg. Additionally, 183 vascular species are non-native plants, which can be further divided into 22 archaeophytes (naturalised non-native plants that arrived prior to 1492), 63 neophytes (naturalised non-native plants that arrived after 1492) and 98 ornamentals (non-native plants that do not have self-sustained populations in Baden-Württemberg). Note that novel plant–insect interactions have been observed between native lepidopterans and non-native plants (Pearse & Altermatt 2013b).

To establish the most probable introduction year, we also assembled estimates of the plant-arrival times in Baden-Württemberg (or, if not available, in Central Europe) based on archaeobotanical and historical records (Sebald *et al.*, 1993–1998; Jacomet & Brombacher 2009; Klotz *et al.* 2002). For each plant, we cross-referenced arrival dates across these sources, additional archaeobotanical records, historical texts such as regional gardening journals, and herbarium and botanic garden records in order establish the most probable introduction year. The arrival times for plants arriving within the last two centuries were precise to 1–10 years. In turn, the arrival times were precise to 50–100 years for plants arriving before the last two centuries and after the middle ages. Similarly, the arrival times for plants arriving before the middle-ages were precise to 100 years. Older records may be conservative estimates, particularly as they are generally based on the oldest remains of these plants to be found.

These aggregated data were stored in a meta matrix (a binary matrix that we called β), where each row i and column j corresponds to an observed plant and an observed herbivore species respectively. Each binary element of this meta matrix represents the presence ($\beta_{ij} = 1$) or absence ($\beta_{ij} = 0$) of an observed plant–herbivore interaction between two species at any point across our observational period. We assumed that there is an interaction between two species as long as there is one record of it in our data. For arrival times, the data were stored as a vector, where each row corresponds to an observed plant species and its value corresponds to the plant's estimated arrival time. Then, for each arrival time t, we formed time-dependent matrices β_t by extracting subsets of the meta matrix, where each plant and herbivore species has an arrival time older or equal than t. Note that herbivore species will be part of a time-dependent matrix as long as any of its host plants is also present (Fig. S1 illustrates how the number of herbivore species changes across time). These time-dependent matrices assume that there is no evolution in or rewiring of interaction preferences between plants and herbivores, that all lepidopterans can be present at any point in time throughout the study area, that depending on the

presence and absence of species all of the possible interactions are always realised at a specific time, and species abundances do not affect the realisation of interactions. While these are strong assumptions (Brändle *et al.* 2008; Faillace & Morin 2016), without empirical information any other simulated process would add *ad hoc* free parameters to our study.

Inferring the competition matrix within the herbivore trophic level

We used the time-dependent matrices β_t to infer the time-dependent competition matrices within the herbivore trophic level (formed by herbivore species competing for host plants) (Saavedra *et al.* 2014, 2017a). Each time-dependent competition matrix (that we called A_t) was inferred by the normalised monopartite projection of the binary matrix β_t (Cenci *et al.* 2018). Specifically, the monopartite projection corresponds to $M_t = \beta_t^T \beta_t$. The off-diagonal entries of the monopartite projection correspond to the number of host plants shared between two herbivores. Thus, the resource overlap between two herbivores i and j is proportional to the matrix element M_{ij} (MacArthur & Levins 1967; Logofet 1993). Normalising the entries of the matrix M_t by the sum of their column (i.e. $A_{ij} = \frac{M_{ij}}{\sum_i M_{ij}}$), we have a time-dependent competition matrix A_t, whose elements can be interpreted as the effect of herbivore species j on species i. That is, if the proportion of shared host plants between herbivore species i and j is high relative to the total number of host plants shared between species i and the rest of the species, the direct effect of species j on species i is high. However, if the two herbivore species do not share any host plants, the direct effect is zero. Note that the effect of species j on i is not necessarily the same as the effect of species i on j. While it has been shown that the persistence of herbivore species depends on many factors, such as: resource availability, the presence of host species, natural enemies and environmental variations, among others (Hairston *et al.* 1960; Gripenberg *et al.* 2007; Tack *et al.* 2009); it has been demonstrated that plant-mediated competition matrices provide explanatory power to the likelihood of herbivore persistence (Saavedra *et al.* 2017a; Cenci *et al.* 2018). Yet, we have not empirically demonstrated that competition occurs in this system, but we are instead assuming that it is an important, but undemonstrated, process in our analysis.

Estimating structural changes within the herbivore trophic level

As we mentioned before, the competition matrix within the herbivore trophic level is time dependent. That is, from the first to the last observed plant arrival, each time t a new plant arrives a new matrix A_t is formed. Thus, to investigate structural changes in A_t across time, we used a comparable measure of structural stability of community persistence. Formally, structural stability corresponds to the extent to which a system can tolerate modifications to its dynamics without changing its qualitative behaviour (Thom 1972). We measured the structural stability of community persistence by the extent to which each competition matrix A_t modulates the range of parameter values (environmental conditions)

compatible with the persistence of all competing herbivores in the community (Saavedra *et al.* 2017b).

To model the competition dynamics among herbivore species, we used a classic Lotka–Volterra (LV) competition model (MacArthur & Levins 1967; Case 2000). Mathematically, the LV dynamics of S competing species can be written as

$$\frac{dN_i}{dt} = N_i(r_i - \sum_{j=1}^{S} a_{ij}N_j),$$

where N_i corresponds to the abundance (or biomass) of species i, r_i is the intrinsic growth rate of species i and a_{ij} are the elements of the competition matrix A_t.

In this competition system, the structural stability of community persistence can be measured by the set of vectors $r = [r_1, r_2, \ldots, r_s]^T$ that guarantees positive species abundances at equilibrium $N_i^* > 0$ as a function of A_t (Saavedra *et al.* 2014; Rohr *et al.* 2016). This parameter space is called the feasibility domain $D_F(A_t)$. The size of this domain can be computed by comparing it against the full parameter space of intrinsic growth rates. Because this domain is compressed of vectors, we are only interested in their direction (not in their magnitude) and the full parameter space can be normalised to a unit ball $\mathbb{B}^S$ made up of vectors with unit magnitude (expressed in terms of a norm). Therefore, the size of the feasibility domain can be calculated by the ratio of the following volumes (Ribando 2006; Saavedra *et al.* 2016b):

$$\omega(A_t) = \left(\frac{2\text{vol}(D_F(A_t) \cap \mathbb{B}^S \cap \mathbb{R}_+^S)}{\text{vol}(\mathbb{B}^S \cap \mathbb{R}_+^S)} \right)^{1/(S-1)},$$

where $\mathbb{B}^S \cap \mathbb{R}_+^S$ represents the normalised S-dimensional parameter space constrained to positive elements in the vectors (i.e. we assumed that species can only take positive intrinsic growth rates (Saavedra *et al.* 2017b)). This ratio can be computed by the cumulative distribution function of a multivariate normal distribution integrated over the positive abundance space (recall that $r = A_t N^* > 0$) and can be efficiently calculated even for relatively large communities (Ribando 2006; Saavedra *et al.* 2016b). The larger $\omega(A_t)$, the larger the fraction of vectors of intrinsic growth rates compatible with the persistence of species at the herbivore trophic level. Thus, $\omega(A_t) \in [0, 1]$ can be used as a comparable quantitative measure of structural stability of community persistence, and can be interpreted as the probability that a randomly chosen species i within the herbivore trophic level characterised by the time-dependent competition matrix A_t can tolerate random environmental changes. Note that our measure of structural stability is not restricted to LV dynamics as long as the dynamics are topologically equivalent (Cenci & Saavedra 2018).

Therefore, to investigate structural changes within the herbivore trophic level, we tracked how $\omega(A_t)$ changes over time by calculating the Pearson correlation between the vectors of structural stability and time, that is, $r(t,\omega(A_t))$. We investigated the robustness of the observed correlation to sampling error by systematically removing a fraction of randomly chosen plants and repeating the analysis above (Legendre & Legendre 2012). Additionally, we performed a split sample test and calculated the corresponding piecewise correlations to evaluate potential nonlinear effects of different observational periods in the assembly order of plants on structural changes within the herbivore trophic level (Legendre & Legendre 2012).

Validating structural stability as a measure of structure within the herbivore trophic level

To test whether structural stability of community persistence can provide a biologically sound description of structure within the herbivore trophic level, we compared the extent to which the structural changes generated by wild self-sustained plants are similar to the changes generated by non-self-sustained ornamental plants. Because our measure of structural stability is linked to community persistence, we hypothesised that ornamental plants, which are non-self-sustained, should play a different role than persistent plants when building the structure within the herbivore trophic level. To measure this, we divided our data into a subset of wild self-sustained plants and a subset of ornamental plants. Then, we used each subset to investigate the corresponding structural changes across time. We calculated the level of similarity in structural changes by the partial Pearson correlation between the two temporal sequences controlling for time t in order to avoid spurious correlations (Iler *et al.* 2017).
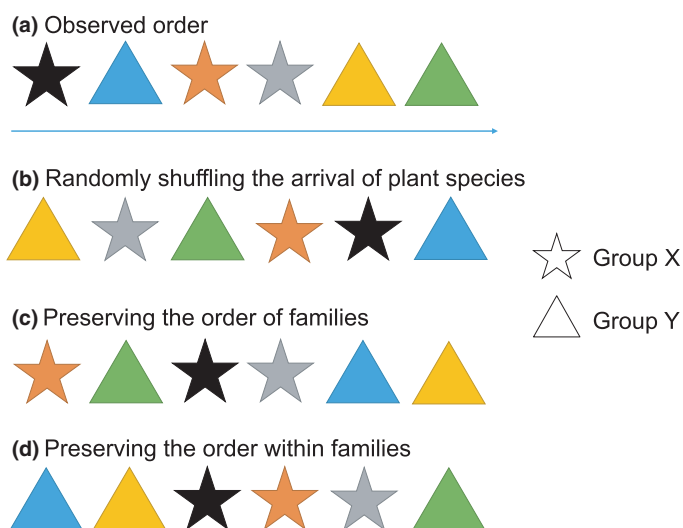
Additionally, to validate that structural changes are not just a by-product of community size, we naively randomised the observed plant arrivals but preserved the observed number of plants per year. Then, we calculated the corresponding distribution of correlations between structural stability and time $r(t,\omega(A_t))$. If structural changes are not an artefact of the number of species and interactions observed in the data, we expected this distribution to be different from the observed correlation. Finally, to illustrate the added value of our measure of structural stability, we repeated the entire analysis using standard global network descriptors (Clauset *et al.* 2004; Pons & Latapy 2005; Almeida-Neto *et al.* 2008). Because it has been shown that these network descriptors fail to capture important differences between structures (Saavedra *et al.* 2017a) and null models cannot be used across different data sets to solve this problem (Song *et al.* 2017), we expected to see no significant differences in time series between wild self-sustained and ornamental plants with these other structural measures.

Testing simple assembly rules acting on the plant trophic level

To investigate the association between the order of assembly in the plant trophic level and structural changes within the herbivore trophic level, we compared the observed correlation between structural stability and time $r(t,\omega(A_t))$ against the statistical ensemble of correlations generated by two random orders of plant arrivals taking into account family-level information. Note that we classified plants according to groups at the family level as they have been found to be among the major determinants of herbivore associations of plants (Ehrlich & Raven 1964; Fox 1987; Pearse & Altermatt 2013b). We have 54 different families in our data. The first random assembly allows the arrival of any plant at any time, but

preserves the order at which families arrive. The second random assembly also allows the arrival of any plant at any time, but preserves the order within families. Note that the number of plants per year is also preserved in both randomisations. Thus, the first and second random assemblies impose hierarchical constraints on the arrival of species from different functional groups (distantly related species) and on the arrivals of species within functional groups (closely related species) respectively. These assembly mechanisms have been broadly investigated (Fox 1987; Fukami *et al.* 2005), and their rationale is based on the observations that diet selection can facilitate the arrival of species from different functional groups until each group is represented before the cycle repeats.

For example, let us classify six plant species *i* into two different families, denoted as X_i and Y_i and $i = 1, 2, 3$. Let us now suppose that the order of arrival is $X_1 Y_1 X_2 X_3 Y_2 Y_3$. This generates structural changes within the herbivore trophic level defined by an ordered vector $[\omega(X_1), \omega(X_1 Y_1), \omega(X_1 Y_1 X_2), \omega(X_1 Y_1 X_2 X_3), \omega(X_1 Y_1 X_2 X_3 Y_2), \omega(X_1 Y_1 X_2 X_3 Y_2 Y_3)]$, which is then correlated to a time vector $[t_1, t_2, t_3, t_4, t_5, t_6]$. Then, testing the constraints introduced by preserving the order of families can lead us to a randomisation such as $X_2 Y_3 X_1 X_3 Y_1 Y_2$, where the order of arrival of species *i* within families X and Y is randomised, but the order at which families arrive is preserved. Similarly, testing the constraints introduced by preserving the order of plant arrivals within families can lead us to a random sequence such as $Y_1 Y_2 X_1 X_2 X_3 Y_3$, where in this case the randomisation occurs across X and Y, but the order of species *i* within its own family remains the same (see Fig. 1 for a graphical example).

(a) Observed order

(b) Randomly shuffling the arrival of plant species

☆ Group X

△ Group Y

(c) Preserving the order of families

(d) Preserving the order within families

Figure 1 Graphical example of random assembly mechanisms for plant arrivals. We considered a hypothetical sequence of plant arrivals with two families (functional groups) X (star) and Y (triangle), and each family contains three species labelled 1,2,3 respectively. Panel (a) shows the hypothesised sequence $X_1 Y_1 X_2 X_3 Y_2 Y_3$, showing that X_1 arrives before Y_1, and Y_1 arrives before X_2, and so on. Panel (b) shows an example of a naive randomisation of the observed arrival sequence by randomly shuffling the order of plant arrivals. Panel (c) shows an example of a randomisation of the observed arrival sequence while preserving the order of families. Panel (d) shows a randomisation of the observed arrival sequence while preserving the order within families.

Because each random assembly generates a distribution of correlations between structural stability and time, we performed a standard likelihood test (Legendre & Legendre 2012) to quantify the extent to which each random mechanism can explain the observed correlation. The distribution of correlations generated by each random assembly is taken as a normal distribution with mean and variance calculated from the simulations. Thus, the likelihood that each random assembly generates the observed correlation is calculated as the probability in the corresponding distribution of the hypothesis. Then, we calculated the ratio between the likelihoods of the first and second random assemblies. Note that ratios > 1 indicate that the order of distantly related plant species can explain better the observed structural changes within the herbivore trophic level, whereas ratios lower than 1 indicate that the observed structural changes are better explained by the order of closely related plant species.
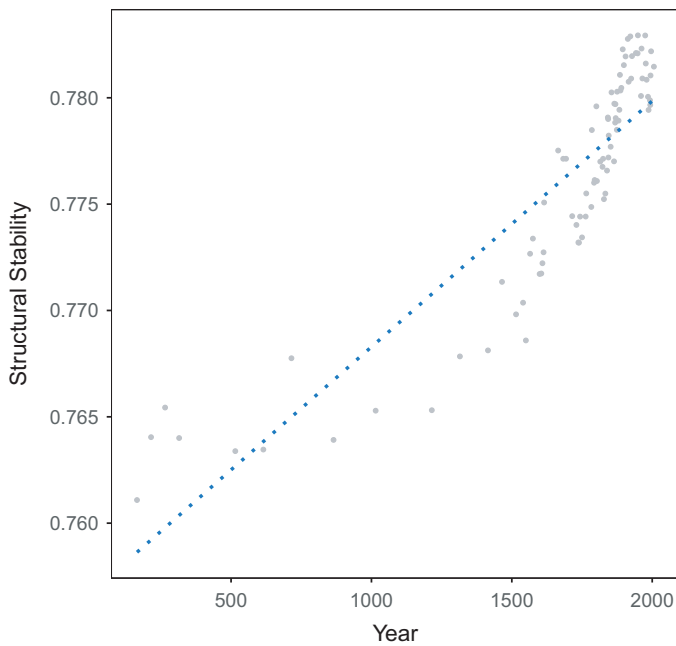
RESULTS

Structural changes within the herbivore trophic level

We found that the observed order of plant arrivals generated a non-trivial increase of structural stability of community persistence within the herbivore trophic level across time. Figure 2 shows that the estimated structural stability given by the inferred competition matrices $\omega(A_t)$ generally increased across the observation period. Specifically, we found a positive trend characterised by a correlation between structural stability and time of $r(t, \omega(A_t)) = 0.89$ ([0.83, 0.92] 95% confidence interval). This positive trend is robust to both potential sampling errors (see Fig. S2) and the split of the time series into two different periods (before and after 1500 AD) (see Fig. S3).

We also found, as expected, that this positive trend is characteristic of wild self-sustained plants, but not of ornamental plants. Figure 3 shows that while structural changes generated by the subset of wild self-sustained plants have a correlation with the overall trend (see Fig. 2) of 0.88 ([0.81, 0.92] 95% confidence interval), structural changes generated by the subset of ornamental plants have a low correlation of 0.27 ([0.07, 0.45] 95% confidence interval). Importantly, the correlation between the structural changes generated by wild self-sustained and ornamental plants is 0.04 (statistically non-significant), confirming that our measure of structural stability can detect differences in the effect of these two groups of plants on the herbivore trophic level. In contrast, standard network metrics fail to detect differences between these two time series (see Figs S4–S7).

Importantly, we found that the positive trend observed for structural stability within the herbivore trophic level is not an artefact of community size and it is highly unlikely to be reproduced by randomly (naively) shuffling plant arrivals (see Fig. 4). In fact, the expected correlation between structural stability and time generated by random plant arrivals is negative (-0.39), revealing that an increase in structural stability within the herbivore trophic level over the entire observation period is highly unlike to be generated by a random assembly of the plant trophic level.

Figure 2 Structural changes within the herbivore trophic level across time. We use the structural stability of community persistence as a measure of structure within the herbivore trophic level. Each point corresponds to the estimated level of structural stability for the inferred competition matrix at a given year $\omega(A_t)$. This figure shows that the estimated structural stability generally increased over time (Pearson correlation of 0.89 with 95% confidence [0.83, 0.92]). The linear-regression line is depicted only to show the trend.

The importance of the order of assembly within plant families

Finally, we found that as long as the order of arrival of closely related plant species is preserved, all the other plant arrivals can happen randomly and still herbivore species would

have been constrained to the same observed structural changes. Figure 4 shows that by randomising plant arrivals while preserving the order of families, the generated distribution of correlations $r(t,\omega(A_t))$ is statistically indistinguishable from zero. In contrast, by randomising plant arrivals while preserving the order within families, all correlations are highly positive as it was observed. In fact, the likelihood ratio of generating the observed correlation between the first and second random assembly mechanisms is 0.1, confirming that only the order of introduction of closely related plant species can explain the observed structural changes within the herbivore trophic level. These results remain qualitatively robust even if we separate the time series into two different periods (see Figs S8–S9).

DISCUSSION

Earlier work has used paleoecological data to show the long-term impact of the order of species arrivals on community composition (presence and absence of species) within trophic levels (Duncan & Forsyth 2006; Mergeay *et al.* 2011). Within this long-term context, our work provides a new direction towards understanding the impact of the assembly order at basal trophic levels on the structure of consumer trophic levels. We have investigated this structure through the lens of structural stability of community persistence, that is, the extent to which the interaction matrix modulates the conditions (parameter values) compatible with persistent herbivore populations. In our study, we have found that the herbivore trophic level generally increased its level of structural stability across time (see Fig. 2). We have found that the order of arrival of closely related (but not of distantly related) plant species constrained the structural changes within the herbivore trophic level as they were observed (see Fig. 4). This implies that if we were to rewind the tape of life and replay it in this community, we should pay particular attention to the factors
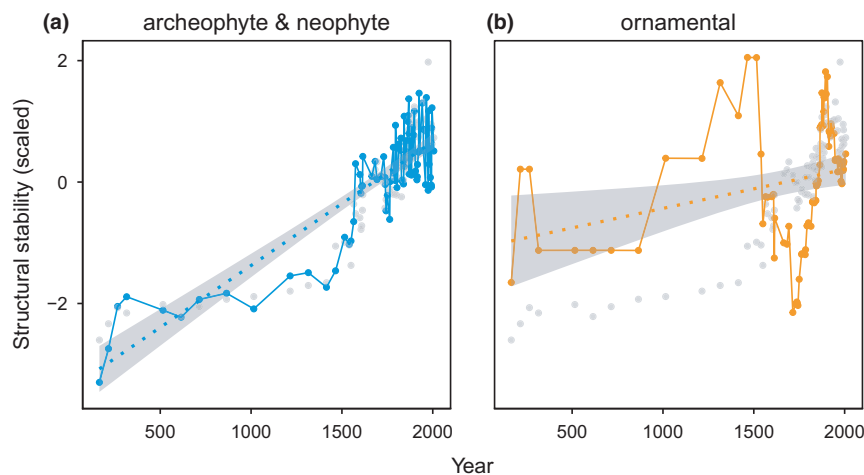
Figure 3 Validating structural stability as a measure of structure within herbivore trophic level. Panels (a) and (b) show (solid lines) the structural changes (measured by the estimated level of structural stability of community persistence) generated by the inferred competition matrices from the subsets of wild self-sustained and ornamental plants respectively. The correlation in Panel (a) is 0.88 ([0.81, 0.92] 95% confidence interval), and the correlation in Panel (b) is 0.27 ([0.07, 0.45] 95% confidence interval). The values of structural stability are scaled for visualisation purposes. The grey points in the background show the pattern generated by the two subsets together (identical to Fig. 2). The linear-regression lines are depicted by shaded 95% confidence intervals.
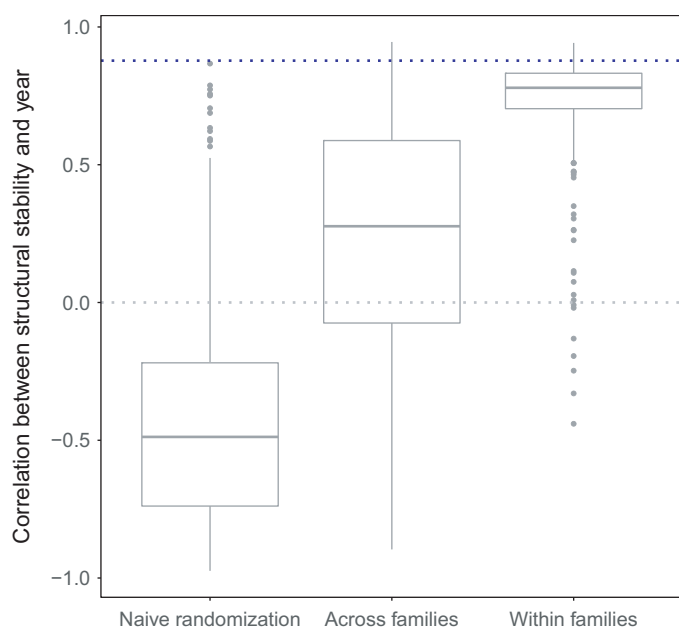
Figure 4 Impact of the plant assembly order on structural changes within the herbivore trophic level. The blue dotted line shows the observed positive correlation of 0.89 between structural stability of community persistence and year $r(t,\omega(A_t))$. The boxplots correspond to the distribution of correlations generated by three random plant assembly mechanisms: randomly shuffling plant arrivals (left boxplot), randomly shuffling plant arrivals while preserving the order at which families arrive (middle boxplot) and randomly shuffling plant arrivals while preserving the order within families (right boxplot). The figure shows that preserving the order of assembly of closely related species (right boxplot) is more likely to generate high positive correlations similar to the observed case. Boxplots depict the interquartile range and the solid line corresponds to the median value. The grey dotted line centred at zero (y-axis) is just intended to serve as a reference guide.

shaping the order at which plants arrive within their own family. Specifically, the existence of alternative structures within the herbivore trophic level may depend on how early arriving plant species affect the arrival of closely related plant species more than they affect the arrival of distantly related plant species.

Our findings above suggest that there are two important ecological mechanisms operating at two different trophic levels. The first mechanism operates at the basal (plant) trophic level and it may be characterised by niche pre-emption – a priority effect acting within functional groups or within similarly competitive species (Fukami 2015). That is, the importance of the order of arrival of closely related plants indicates the effect of a strong pre-emption (hierarchical) mechanism acting within functional groups of plants. This pre-emption mechanism within families can arrive during successional development as a consequence of already highly exploited niches (Odum 1969). Alternatively, this ordering may be the outcome of a non-random presence of propagule pressure in which generalist host plants tend to arrive earlier than specialists (Pearse & Altermatt 2013b). Note that we did not explicitly model competition among plants. Instead, we modelled the process of diversification of host plants through the randomisation of the order of plant arrivals. This assumes

that the assembly process of the plant trophic level converges to the same community composition at the end of the observation period.

The second mechanism operates at the consumer (herbivore) trophic level and it may be the result of the dynamics acting at the lower (plant) trophic level. That is, our data revealed a positive trend of structural stability of community persistence within the herbivore trophic level over 2000 years (see Fig. 2). Recall that the higher the level of structural stability, the larger the tolerance of a community to random environmental changes. Because our definition of structural stability is inversely related to the overall level of resource overlap (Rohr et al. 2016; Cenci et al. 2018), the observed non-trivial positive trend also indicates a non-trivial increase in resource partitioning. This implies that the herbivore community favoured structures with high overlap of host plants during the early assembly stages, but this overlap dilutes as the community matured. Importantly, this trend can be attributed to the observed order of plant arrivals within families (see Fig. 4). Without preserving any order of arrivals, our simulations have revealed that the structural stability of the community would have decreased over time. Similarly, by only preserving the order of arrivals across families (but not within), on average there would have been no trend whatsoever. Therefore, an observed increase of structural stability in the herbivore community for over 2000 years may indicate potential non-adaptive dynamics as the result of the particular constraints imposed by the plant trophic level (acting as environmental conditions) (Tregonning & Roberts 1979; Borrelli et al. 2015; Saavedra et al. 2016a; Song et al. 2017).

Focusing on the observed trend of structural stability of community persistence (Figs 2 and S3), it is worth noting that the breakpoint around the year 1500 A.D. may have various ecological consequences, such as an increase in the number of non-native plants, as well as a the arrival of plants from a previously completely disconnected biogeographic area, namely the Americas (see Fig. S1). Unfortunately, we do not have knowledge on systematic ecological differences between these plants, but clearly they represent some previously separated pools of species that may have different effects on the structural stability of the system. Yet, our randomisation results have indicated that no single species is responsible for the observed trend of structural changes within the herbivore trophic level. This has been confirmed by noticing that a naive random assembly cannot generate a positive trend of structural stability across time (see Fig. 4). Thus, the impact of a newly introduced species on the structure of a community is time dependent, especially an order-dependent process within functional groups. This can be the reason why many times invasive species are found without significant impact on the structure of a community when analysed using non-temporal data (Stouffer et al. 2014). Overall, our results imply that structural changes within consumer trophic levels may be explained and anticipated by assembly rules within functional groups operating on basal trophic levels and the environmental pressures acting on the focal trophic level. Thus, future work should focus on disentangling the impact of these two forces on the structure and dynamics of trophic levels.

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COMPETING INTERESTS

The authors declare no competing financial interests. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

AUTHOR CONTRIBUTIONS

All authors designed the study and analysed data. CS performed the study. SS supervised the study. CS and SS wrote a first version of the manuscript. All authors contributed with substantial revisions. FA and IP compiled and provided data.

DATA ACCESSIBILITY

Data and R-code supporting the results can be found on Github: https://github.com/clsong/ELESong_et_al2018

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.