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Diversity, food web structure and the temporal stability of total plant and animal biomasses

Jérôme Eschenbrenner and Élisa Thébault

J. Eschenbrenner (https://orcid.org/0000-0003-4279-1819) ✉ (jerome.eschenbrenner@inrae.fr) and É. Thébault (https://orcid.org/0000-0002-9669-5227), Sorbonne Université, CNRS, IRD, INRAE, Université Paris Est Créteil, Université Paris Cité, Institute of Ecology and Environmental Sciences of Paris (iEES-Paris), Paris, FranceSorbonne Univ., Univ. Paris Est Créteil, Univ. de Paris, CNRS, INRAE, IRD, Inst. d'Écologie et des Sciences de l'Environnement – Paris, iEES-Paris, Paris, France. J. E. also at: INRAE, Aix Marseille Univ, RECOVER, Aix-en-Provence, France.

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Food-web complexity and species richness are predicted to have tremendous effects on ecosystem functioning stability. Yet, our understanding of the relation between diversity and the stability of ecosystem functioning is still mainly limited to single trophic level communities and highly simplified food webs. To start filling this knowledge gap, we model allometric food webs and use structural equation modelling (SEM) to investigate the relations between diversity, food web structure and the temporal variability of total plant and animal biomasses and their components, i.e. synchrony and mean population variability. We find that stability responds differently depending on the metric used. When looking at total biomass variability, higher total biomasses and biomass stored at higher trophic level have the strongest stabilising effects, while species richness has lower impact than previously found. We confirm that synchrony among species is important for the stability of the total plant biomass. However, synchrony only weakly explains variations in the stability of total animal biomass among food webs. Species richness and food web variables often have opposite impacts on synchrony and mean population variability, leading to more ambiguous results for the plant community as synchrony matters only for plant stability. Our approach thus provides new insight on the complexity of the stability of ecosystem functioning in complex food webs.

Keywords: diversity, ecosystem functioning, food webs, stability, temporal stability, theory

Introduction

The study of the relationship between biodiversity and ecosystem functioning (BEF) has been – for the last three decades – a key field in ecology, aiming to understand the consequences of global changes on biodiversity, and thus ecosystem processes, in a concern for improving ecosystem conservation and management. BEF has been studied especially on functions like biomass production, decomposition, pollination or carbon sequestration (Cardinale et al. 2012, Schneider et al. 2016, van der Plas 2019), and on the stability of these functions, often measured as the inverse of the coefficient of variation of ecosystem properties over time (Tilman et al. 2006, Hector et al.

2010). Overall, studies have found positive relationships between diversity and stability of ecosystem functions, especially for the total biomass (Tilman et al. 2006, Hector et al. 2010, Xu et al. 2021), even if non-significant relationships are also common (Hooper et al. 2005, van der Plas 2019). This positive effect of diversity is most likely due to asynchrony among populations, partly in relation to species differences in response to disturbances (Lehman and Tilman 2000, Hooper et al. 2005, Tilman et al. 2006, Loreau and de Mazancourt 2008, Hector et al. 2010, van der Plas 2019).

While we have gained extensive knowledge in the field of biodiversity and ecosystem functioning (BEF) for plant communities (Lehman and Tilman 2000, Tilman et al. 2006, Loreau and de Mazancourt 2008, Jiang and Pu 2009, Hector et al. 2010), studies looking at the importance of the whole food web structure on ecosystem functioning have been more sparse (Thébault and Loreau 2005, Schneider et al. 2016, Wang and Brose 2018, Zhao et al. 2019, Maureaud et al. 2020, Quévreux et al. 2021) although the distribution and the strength of trophic interactions have tremendous effect on the flux of matter and energy in ecosystems. As a growing number of experimental and empirical studies investigate BEF relationships in either simplified food webs or animal communities (Jiang and Pu 2009, Blüthgen et al. 2016, Olivier et al. 2020, Danet et al. 2021), understanding the mechanisms behind these relations becomes particularly important. Indeed, some studies suggest that BEF relations might differ between single-trophic and multi-trophic communities (Duffy et al. 2007, Jiang and Pu 2009, Danet et al. 2021).

Theoretical studies on the links between diversity and ecosystem functioning show that the effects of diversity are complex in food webs, and depend on the ecosystem processes considered (Thébault and Loreau 2006, Schneider et al. 2016, Maureaud et al. 2020), on average species generalism in the food web (Thébault and Loreau 2006, Maureaud et al. 2020), on species body mass distribution (Schneider et al. 2016) and on the number of food web trophic levels (Wang and Brose 2018). However, while recent models have brought new insights on the relationships between diversity and ecosystem properties in food webs, the stability of these properties has been largely ignored in this context. This is surprising because the stability of food webs have traditionally received a lot of attention in theoretical ecology since the study of May (1972). This gap of knowledge is due to the fact that food web stability has been mostly considered using descriptors that strongly differ from those investigated in BEF experiments and observational studies (e.g. local stability versus temporal variability, Donohue et al. 2016), and using often 'species-poor' models (Kéfi et al. 2019). To our knowledge, there are no studies explicitly looking at the relationship between diversity, food web structure and the stability of ecosystem functioning in 'complex' (i.e. species-rich) food web models. There is thus a need to extend recent studies on BEF relations in food webs to the study of the temporal variability of ecosystem properties. For instance, species diversity, food web connectance and the number of trophic levels are expected to greatly affect the stability of ecosystem functioning in food webs, because existing theoretical studies have highlighted the importance of diversity, connectance and the presence of top predators for several measures of food web stability (May 1972, Kondoh 2003, Allesina and Tang 2012, Shanafelt and Loreau 2018). Similarly, predation links can strongly affect synchrony (McCann and Rooney 2009) that is a main component of the stability of ecosystem properties (Thibaut and Connolly 2013), and we might expect this effect to be amplified in food webs.

To explore the relationship between diversity, food web structure and the stability of ecosystem functioning, we considered the temporal variability of both the plant and animal total biomasses using a food web model with body-mass constraints (Schneider et al. 2016). Allometric constraints are important to take into account in this context as these are known to affect many species traits such as metabolic and feeding rates, with wide consequences on both ecosystem processes and food web stability (Binzer et al. 2016, Schneider et al. 2016). We did not include stochasticity in our model, thus the temporal variability of biomass only results from intrinsic predation and competition processes and not from perturbations. Even though it is well known that stochasticity and species responses to environmental perturbations are important for ecosystem stability, and especially synchrony (Loreau and de Mazancourt 2008, van der Plas 2019), food web complexity and predation are still key and overlooked processes to determine ecosystem stability (Halpern et al. 2005, Benincà et al. 2009, McCann and Rooney 2009, Gross et al. 2014, Shanafelt and Loreau 2018), and we did not want to mix them to not over-complexify the model. To favour comparison between our theoretical results and empirical ones, we followed the same statistical approach as recent studies on the stability of animal communities (Blüthgen et al. 2016, Olivier et al. 2020, Danet et al. 2021). Specifically, we studied the relations emerging from our model between species richness, food web structure (measured by weighted connectance and average trophic level weighted by biomass) and stability, as 1) probability of local stability and 2) the two components of the temporal stability of total biomass that are population stability and synchrony (Thibaut and Connolly 2013, Olivier et al. 2020, Danet et al. 2021, Xu et al. 2021). In addition, we also considered total plant and animal biomasses in this analysis as it is still debated whether the effects of species richness on total biomass and its stability are independent or not (Cardinale et al. 2013, Wang et al. 2021). Please note that hereafter we refer to primary producers and consumers as plants and animals for the sake of simplicity.

Material and methods

Model description

The model used here is based on the allometric food web model developed by Schneider et al. (2016). This model has been previously used to investigate the relationship between animal richness and ecosystem functioning in food webs. It is thus well suited to study the links between species richness, food web structure, biomass and the stability of ecosystem functioning. The model comprises two nutrients, several species of primary producers that compete for nutrients, and several animal species that can be herbivores, predators of other animals or both. The original equations and parametrisation of the model were left untouched. The complete description of the model can be found in Schneider et al. (2016) and in the Supporting information, and only the main components and hypotheses of the model are summarized below.

The known relations between species body mass and species functional and demographic traits are central to the model. Species body mass determines its growth rate, metabolism and feeding rates on the other species in the community, resulting in complex food webs. Animal species predate on the smaller species (both plants and animals) that are falling in their optimal range of prey body masses, which is defined around 100 times smaller than them.

The dynamics of each nutrient (N_l) and of the biomass of each plant (P_i) and animal (A_i) species are defined by the following equations (Schneider et al. 2016):

$$\frac{dN_l}{dt} = D\left(S_l - N_l\right) - \nu_l \sum_{i=1}^{n_P} r_i G_i P_i \text{ for } l \in \left\{1,2\right\} \tag{1a}$$

$$\frac{dP_i}{dt} = r_i G_i P_i - \sum_{j=n_P+1}^{n_P+n_A} A_j F_{ji} - x_i P_i \text{ for } 1 \le i \le n_P \tag{1b}$$

$$\begin{aligned}\frac{dA_i}{dt} = {} & e_P A_i \sum_{j=1}^{n_P} F_{ij} + e_A A_i \sum_{j=n_P+1}^{n_P+n_A} F_{ij} - \sum_{j=n_P+1}^{n_P+n_A} A_j F_{ji} \\ & - x_i A_i \text{ for } n_P + 1 \le i \le n_P + n_A\end{aligned} \tag{1c}$$

with n_P and n_A the number of species of plants and animals respectively, D the nutrients' turnover rate, S_l the supply concentration of nutrient l, v_l the nutrient relative content in plants, r_i the plant growth rate, x_i the plant and animal metabolic losses, e_p and e_A the conversion efficiency (on plants or animals respectively) and F_{ij} the feeding rate of consumer species i on prey species j, which can be either a plant ($j \in \{1, \ldots, n_P\}$) or an animal ($j \in \{n_P + 1, \ldots, n_P + n_A\}$). The growth rates, metabolic losses and feeding rates depend on the body mass of the species. The feeding rate is defined by a functional response which varies in-between a Holling-type II and III functional response and includes intraspecific predator interference (Schneider et al. 2016). Other equations and parameters, including the definition of the functional response, are further described in the Supporting information.

To assess the correlations between species richness, food web structure, total biomasses and the temporal variability of ecosystem functioning, we performed numerous simulations of the food web dynamics, of which we discarded the ones where, at any point in time, a plant was left with no predator, for a final total of 15 453 simulations. Non-edible plants indeed had a huge impact on ecosystem functioning, and were not the subject of this study, we thus removed them similarly to Schneider et al. (2016). In order to study of stability of food webs with varying species richness and structure, simulations started with varying numbers of animal species (10–60) and plant species (15–44), randomly drawn in a uniform distribution. In each simulation, each species was attributed a random body mass, which ranged from 10^0 to 10^6 for plants and from 10^2 to 10^{12} for animals, with the exponent being drawn in a uniform distribution, and with the smallest possible body size equal to unity (i.e. same body size scaling as used in Schneider et al. 2016). The simulations were run for 100 000 steps, using the Euler method for integration, with a step size of 0.001. The accuracy of the Euler method – which can be fairly imprecise if the step size is not small enough – has been checked by carefully comparing our results with same simulations but with smaller time steps or with the same time step but a more efficient Runge–Kutta method. We choose to use this integration method to ease the use of our code by future studies requiring Euler-like methods, as required when including stochasticity (Shanafelt and Loreau 2018). Note that at the end of the run, once the transient dynamics were over and an equilibrium was reached, several species were often extinct. A species was considered extinct and its biomass set to 0 if its biomass was below an extinction threshold, set to 10^{-6}.

Descriptors of ecosystem stability and food web structure

To assess the relations between species richness, food web structure, total biomasses and temporal stability of ecosystem functioning, we focused on the last 5000 time steps of the simulations, the descriptors being averaged over these time steps. Our analysis showed that the descriptors measured were not different from the same descriptors averaged 5000 steps before those, showing that the transient dynamics were over, even if the system is not necessarily at a stable equilibrium but keeps fluctuating. All descriptors (when applicable) were calculated for plants and animals separately. Indeed, we do not expect plant and animal stability to react similarly to plant and animal richness, as found previously for total plant and animal biomasses (Schneider et al. 2016).

Diversity was described by both plant and animal species richness at the equilibrium, after the initial extinctions during transient dynamics. We considered two common food web descriptors, out of the numerous that have been developed. First, we calculated an index of weighted connectance as a function of the Shannon diversity of feeding links (Supporting information). Second, we quantified the trophic level where most of the biomass is stored on average by calculating the mean weighted trophic level in the food web. To do so, for each food web, we calculated species trophic levels using the feeding rates (Supporting information) in order to take into account the actual feeding range of predators into the calculation of each species trophic level. Species trophic levels were then averaged and weighted by the biomass of each species (Supporting information).

As often done by BEF experimental and empirical studies, we measured ecosystem functioning as the total biomasses of plants and animals and ecosystem stability as the temporal variability of these two types of total biomasses (Tilman et al. 2006, Hector et al. 2010, Olivier et al. 2020, Danet et al. 2021). Temporal variability of total biomass was here defined by the coefficient of variation, calculated as $\mathrm{CV} = \sigma/\mu$, μ being the mean biomass over the time period considered and σ the standard deviation. A higher CV indicates more variability in the biomass, and thus less stability. A CV of 0 indicates that the biomass is at a stable equilibrium.

A number of simulations of food web dynamics lead to a stable equilibrium, as indicated by CV values equal to 0, whereas in other simulations the equilibrium was unstable with oscillations in species biomasses and non-zero CV values. Diversity and food web structure can show different effects depending on the stability measure considered (Donohue et al. 2016). We thus conducted two different analyses on the CV of total biomasses by first considering the effects of species richness and food web structure on the probability of food web local stability (i.e. $\mathrm{CV} = 0$), and second by studying the effects of the same variables on the values of the total biomass CVs of the unstable food webs.

To study the probability of food web local stability, we created a binary variable equal to 1 if the total biomass CV of the system was 0 (stable) and to 0 otherwise. For the unstable webs where CVs are non-null, the CV of the total biomass (later referred as total biomass stability) can be decomposed into, as proven in Thibaut and Connolly (2013), 1) the mean CV of the species biomass weighted by their abundance $\overline{\mathrm{CV}_w}$ (later referred as mean weighted population CV) and 2) the squared root of synchrony among species, φ, defined by Loreau and de Mazancourt (2008), as:

$$\mathrm{CV} = \overline{\mathrm{CV}_w} \times \sqrt{\varphi} \tag{2a}$$

with

$$\overline{\mathrm{CV}_w} = \sum_i \frac{\mu_i}{\mu} \mathrm{CV}_i \tag{2b}$$

and

$$\varphi = \frac{\sigma^2}{\left(\sum_i \sigma_i\right)^2} \tag{2c}$$

with μ and σ being respectively the mean biomass and the standard deviation of the community, and μ_i and σ_i being respectively the mean biomass and the standard deviation of the species *i*. These three measures correspond to different aspects of stability and are important to characterize the state of the system, namely describing the temporal variability of the communities (the temporal stability of the system), the temporal variability of the populations (the temporal stability of the components of the system) and the synchrony of their dynamics (the stability also arising from asynchrony among the components).

Statistical analyses

Using the equilibrium dynamics of the 15 453 food webs studied, we investigated the relations between: 1) plant and animal richness; 2) food web structure measured by weighted connectance and mean weighted trophic level; 3) total plant and animal biomasses; and 4) our two measures of the stability of total plant and animal biomasses that are the probability to be locally stable and the total biomass CV of plants and animals for unstable webs. As total biomass CV can be decomposed into the mean weighted population CV and the synchrony, the relative importance of these two stability components were further considered in the case of unstable food webs. To study the relations among all these variables, we used structural equation modelling (SEM), with path analyses. SEMs allow investigating the potential causal direct and indirect relations among multiple variables, and they have been increasingly used in the last decade to assess the links between diversity, community structure and community stability (Blüthgen et al. 2016, Olivier et al. 2020, Danet et al. 2021). By using this approach, we thus ease the comparison between our results and those from empirical studies on ecosystem stability.

To define the SEMs, we hypothesized that species richness directly affects stability (Tilman et al. 2006, Hector et al. 2010) as well as food web structure (Kondoh 2003, Allesina and Tang 2012, Shanafelt and Loreau 2018) and total biomass (Cardinale et al. 2013, Schneider et al. 2016, Wang et al. 2021). We further assumed that food web structure directly affects stability and total biomass (McCauley et al. 2018, Wang and Brose 2018, Maureaud et al. 2020). For instance, greater connectance is expected to decrease the probability of food web stability (May 1972) but it might also decrease predator population variability as predator generalization can dampen the destabilizing effects of prey fluctuations (Thébault and Loreau 2005). In addition, the presence of species at higher trophic levels can increase total biomass by increasing the total nutrient uptake in food webs (Wang and Brose 2018) but it can also increase the temporal variability of prey populations (Shanafelt and Loreau 2018). Meanwhile, total biomass and its distribution among trophic levels is also assumed to be linked to stability as higher consumer to resource biomass ratio has been shown to increase the temporal variability of food web biomass (McCauley et al. 2018). For the SEMs on the total biomass CVs of unstable webs, the variables were linked only to the weighted mean species CV and the synchrony, because those two fully mathematically determine the total biomass

CVs (Eq. 2a). While we acknowledge that other variables play a role in shaping the stability of food webs (such as the shape of the feeding function), and that the variables used here can influence each other retroactively, this SEM reflects main hypotheses on the links between species richness, food web structure, total biomass and its stability.

The SEMs were performed using R and the package piecewiseSEM (Lefcheck 2016). All variables were log-transformed in order to better fulfil model requirements (see the full description of model equations in the Supporting information and the plots of the relations among studied variables and residual plots in the Supporting information). We used classical linear models to study the relations among all variables, except to study the probability of food web local stability, which was a binary variable, for which we thus used a generalised linear model with a binomial family. We tested the multi-collinearity of the variables of each model in each SEM with variance inflation factor (VIF) analysis (Supporting information). We found that the very strong correlation between the mean weighted trophic level and the total animal biomass was causing problems for being too high (correlation = 0.87, VIF > 5). We thus removed the total animal biomass from all SEMs, which did not affect the main results, while still discussing the effects of total animal biomass on stability and its relations with other food web variables. The slopes from the SEMs and the summed effects shown in the figures were standardised to allow comparisons. The paths whose slope had a p-value larger or equal to 0.05 were not shown in the figures. Indirect effects between two variables were calculated by multiplying the slope in all possible paths that were then all summed together, while total effects were computed by summing all direct and indirect effects.

According to the mathematical relation between the CV of total biomass, the mean weighted CV of species biomass and synchrony (Eq. 2a), and because we performed a log transformation of these variables, the unstandardised coefficients of the SEMs are equal to 1 for the predicted effects of the mean species CV and 0.5 for the effects of synchrony. However, we consider standardised coefficients in the following to compare the magnitude of the effects of the different variables. While we expect the relative importance of the mean species CV and the synchrony to explain the community CVs following a 1–0.5 ratio, deviations from this would indicate that one of the two components of community stability (either mean weighted species CV or synchrony) is more variable than the other among food webs, and thus contribute more than expected to variations in community temporal stability among simulated food webs.

Results

Relations between species richness, food web structure and total biomasses of animals and plants

The SEMs first highlight the emerging relationships between species richness, food web structure and total biomass among our simulated food webs (Fig. 1a). Animal richness is positively related with both food web weighted connectance and the mean weighted trophic level, which indicates that food webs with higher animal richness are characterized by higher connectance and species biomass at higher trophic levels. To the contrary, plant richness is mainly associated with decreased connectance. Our results also suggest that the relations between species richness and total biomass are mostly indirect. Animal richness also has a net positive effect on total animal biomass, which can be inferred from the strong positive relation between the mean weighted trophic level and total animal biomass (cor = 0.87). Animal richness has a weak net negative effect on total plant biomass (summed standardized effects = −0.17), which is mediated through the negative relations between connectance and total plant biomass as well as between the mean weighted trophic level and total plant biomass. Plant richness has almost no effect on mean weighted trophic level and associated total animal biomass and only weak positive net effects on plant biomasses (summed standardized effects of 0.02 on mean trophic level and 0.20 on total plant biomass), which are mainly mediated through its negative relation with connectance for total plant biomass.

Local stability of total plant and animal biomasses

Out of the 15 453 simulations, 7606 (48%) lead to an equilibrium that was locally stable for both total plant biomass and total animal biomass. As could be expected, the local stability of total plant and animal biomasses (i.e. $CV_{pA} = 0$ and $CV_{oA} = 0$) were strongly correlated: there were only 0.49% of the simulations where plant total biomass only was unstable and 0.5% where animal total biomass only was unstable. Thus, the results in this section are presented grouped for both animals and plants.

Overall, the probability of local stability is related to relatively weak and mostly independent (i.e. direct) effects of species richness and food web structure while it is not significantly related to total plant biomass. While higher plant and animal richness and higher connectance promote the occurrence of unstable dynamics (Fig. 1), a high weighted trophic level (and related total animal biomass) favour local stability.

Temporal variability of total plant and animal biomasses

The analyses of the values of total biomass CVs were done on the subset of unstable food webs (n = 7847). The results reveal that the CV of total animal biomass is related to different variables than the CV of total plant biomass in our simulated food webs.

Regarding the total animal biomass CV, the SEM indicates that the variations in the CV of total animal biomass are mostly explained by the variations of the mean weighted animal population CV among food webs, rather than by the variations in synchrony (respectively 0.98 and 0.17, Fig. 2b, Supporting information). The synchrony has less importance than expected from the mathematical relation, where we expect the synchrony to be half as important as the mean

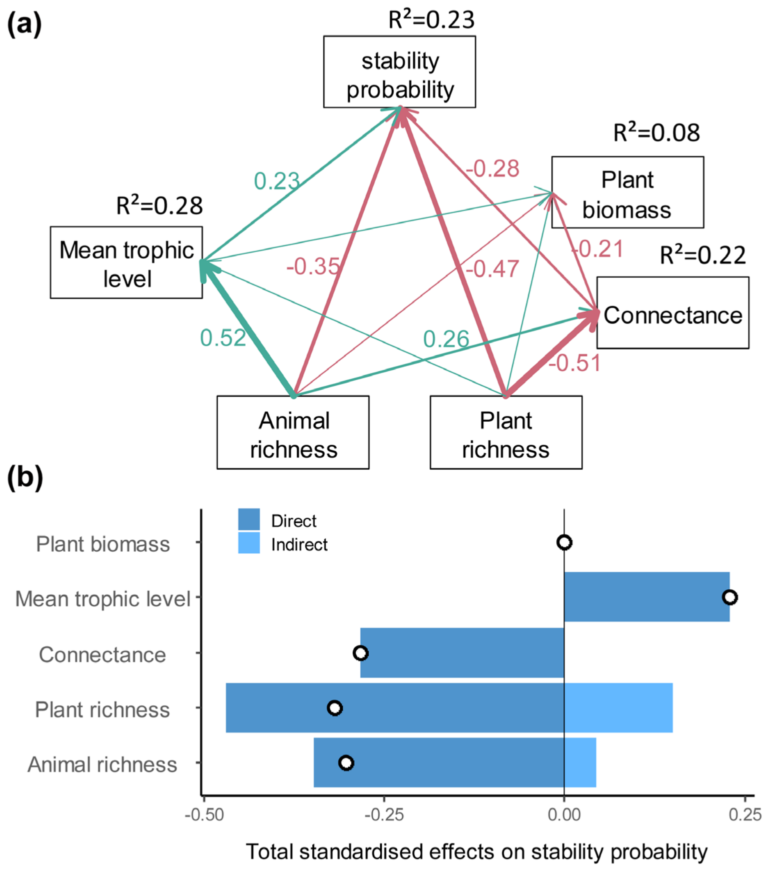

Figure 1. Effects of species richness, food web structure and total biomass on the probability of a web to be locally stable. (a) SEM. Arrows thickness is proportional to the absolute standardised coefficients, red arrows represent negative relationships and green arrows positive ones. Non-significant relationships and values below 0.1 are not shown. With adjusted R^2, approximated by the McFadden's pseudo-R^2 for the stability probability. (b) Standardised direct and indirect effects of the variables on the probability of food web local stability. The dots represent net effects. Indirect effects from a given variable on stability probability are computed by multiplying the standardised coefficients along each path, and then are summed over all the paths joining the given variable and stability probability.

weighted population CV in determining the total biomass CV (according to the Eq. 2a and the log transformations). Thus, the variables that are mostly related to the stability of total animal biomass are those that affect directly or indirectly animal population CV. The mean weighted trophic level has a strong direct negative relation with mean weighted population CV, which indicates that food webs with biomass stored at high levels are characterized by low mean animal population CV and thus higher stability of total animal biomass, similarly to food webs with high total animal biomass (Fig. 2b, d). Food webs with greater animal richness (by indirect effects through the trophic level metric) and with greater total plant biomass show higher stability of total animal biomass (Fig. 2d). Meanwhile connectance has almost no net effect on the CV of total animal biomass, and plant richness has a small destabilising impact (Fig. 2d).

For the CV of total plant biomass, the relative importance of the mean weighted population CV and the synchrony is as expected from the mathematical relation (respectively 1.07 and 0.55, Fig. 2a, Supporting information), as explained in the methods. This means that contrary to animals, variation in synchrony matters for the variation of plant community stability among simulated food webs. Plant total biomass and animal richness have respectively clear stabilising and destabilising impacts on the total plant biomass (Fig. 2c). Weighted connectance has a weak net destabilizing effect on total plant biomass, mediated through its negative relation with plant biomass. The SEM indicates that mean weighted trophic level, which is strongly related with total animal biomass, and plant richness have relatively weak net destabilizing effects on the total plant biomass despite their strong relations with weighted plant population CV and synchrony (Fig. 2c). This is due to the fact that the mean weighted trophic level, total animal biomass and plant richness have opposite impacts on the synchrony and the mean weighted population CV for the plant community (Fig. 2c, 3). The Fig. 3 illustrates this well: while an increase in the total animal biomass leads to a decrease in the mean plant population CV (and thus an increase in stability, Fig. 3a), it also leads to an increase in plant synchrony (and thus a decrease in stability, Fig. 3b), giving an overall weak and hump-shaped relation between the total animal biomass and the temporal stability of the plant community (Fig. 3c).

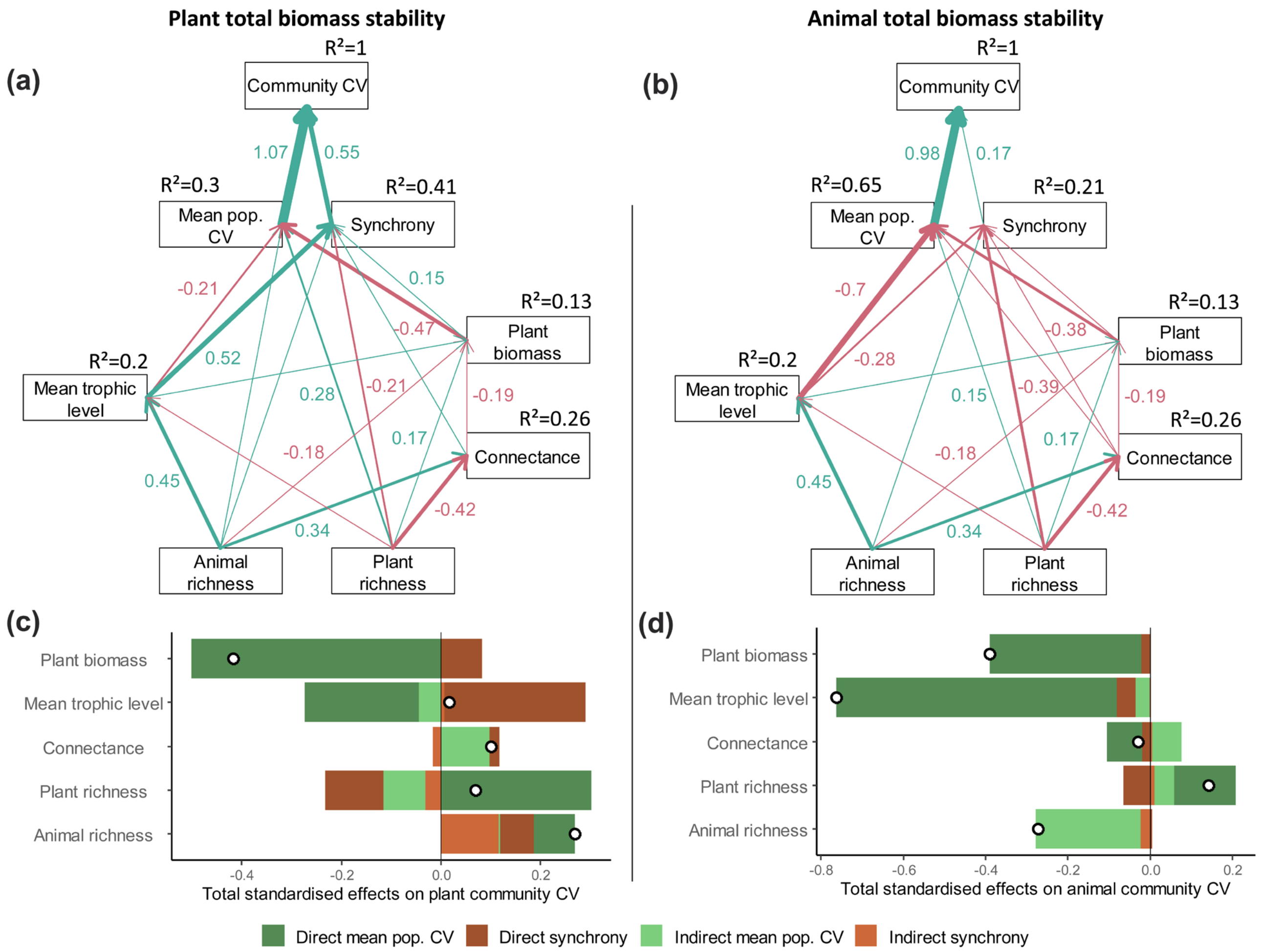

Figure 2. Effects of species richness, food web structure and total biomass on the stability of total plant (a and c) and animal (b and d) biomasses. (a and b) SEM. Arrow thickness is proportional to the absolute standardised coefficients, red arrows represent negative relationships and green arrows positive ones. Values below 0.15 are not shown and non-significant relationships had their links removed. R^2 corresponds to adjusted R^2. (c and d) Standardised direct and indirect effects of the variables on the stability of total plant and animal biomasses, as mediated through mean weighted population CV and synchrony. The dots represent net effects. Indirect effects from a given variable on another are computed by multiplying the standardised coefficients along each path, and then are summed over all the paths joining the two variables. For all six stability measurement here, a higher value means less stability.

Discussion

We simulated the dynamics of an allometric food web model and investigated the relations between species richness, food web structure and ecosystem functioning stability, by studying the temporal stability of total plant and animal biomasses. First, our results on the biodiversity–biomass relationship corroborate previous findings. Animal richness both strongly increased animal biomass and slightly decreased plant biomass, as we could expect from cascading effect (Schneider et al. 2016). Plant richness increased total plant biomass, which is a common result (Jiang and Pu 2009, Cardinale et al. 2012, van der Plas 2019). Second, we found that the effects of species richness and food web structure differed among stability metrics (probability of local stability versus CV of total biomass) and ecosystem functions (plant versus animal total biomasses). While animal richness was clearly related with lower total animal biomass CV and higher plant biomass CV, plant richness had weak destabilizing effects. Meanwhile, the mean weighted trophic level (which was strongly correlated to total animal biomass) was strongly related to total animal biomass stability, whilst weighted connectance had almost no effect on CVs, but decreased the stability probability similarly to species richnesses.

The diversity–stability relationship

Our findings first highlight an overall positive effect of animal richness on the stability of total animal biomass, as defined by the inverse of the CV of total biomass, which results from a decrease in mean animal population variability at high animal richness. This finding complements the positive effect of animal richness on total animal biomass previously predicted with the same allometric food web model (Schneider et al.

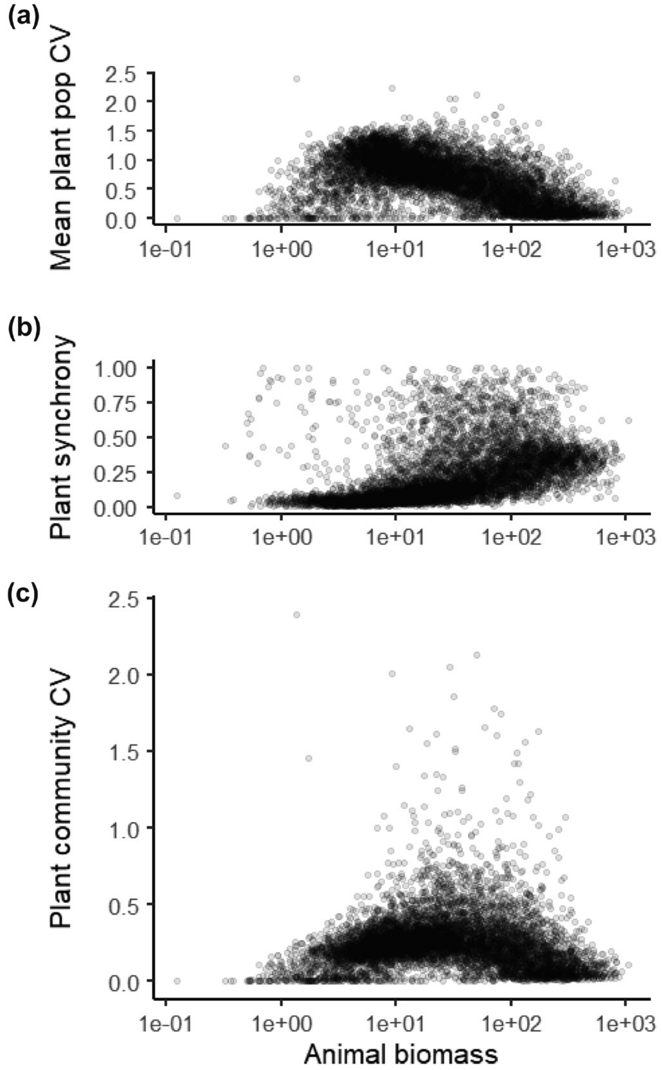

Figure 3. Relation between the total animal biomass and the three descriptors of plant stability, respectively the mean plant population CV (a), the plant synchrony (b) and the plant community CV (c). For all panels, a higher y value means less stability.

2016). It is also in agreement with the results of a meta-analysis on the stability of populations and communities (Jiang and Pu 2009), suggesting that species richness decreases temporal variability at both population and community level in multi-trophic systems. Our results might be partly explained by changes in species body mass distribution with species richness, due to larger average individual plants and animals at high animal richness (Schneider et al. 2016). Indeed, species body mass distribution is known to affect food web stability (Brose et al. 2006), and food webs with higher mean individual body mass tend to show lower CV of total biomass at both plant and animal levels in our simulations (Supporting information).

While animal richness is positively related with the stability of total animal biomass, we found that plant and animal richness have a weak destabilising effect on total plant biomass and that plant richness slightly destabilizes total animal biomass as well. These results differ from general findings on the effects of plant richness on the temporal stability of total plant biomass. It is indeed widely admitted that, for plants, diversity often stabilises the community (Lehman and Tilman 2000, Hooper et al. 2005, Tilman et al. 2006, Ives and Carpenter 2007, Loreau and de Mazancourt 2008, Griffin et al. 2009, Hector et al. 2010, Gross et al. 2014, van der Plas 2019, Xu et al. 2021). Our contrasting results might first be explained by the fact that the relation between diversity and ecosystem functioning and its stability differ between food webs and single-trophic level communities (Duffy et al. 2007, Jiang and Pu 2009, Zhao et al. 2019). Our results are indeed consistent with the results of a two-trophic food web model showing that consumer diversity can destabilize the stability of total plant biomass whilst it stabilizes total consumer biomass (Thébault and Loreau 2006). The importance of trophic interactions for the relation between diversity and the stability of ecosystem functions is further exemplified by the results of our path analyses because effects of species richness are partly mediated by effects of food web structure on stability. Studies on the relation between diversity and the stability of ecosystem functioning in food web models have unfortunately been scarce, which prevents more in-depth comparison with previous findings.

Second, the weak effects of species richness on the variability of total biomasses we observed, apart from the effect of animal richness on total animal biomass CV, might also be explained by the fact that species diversity only results from differences in species body mass in our model. Allometric parametrising brings more realism to food web models and this approach has brought important insights on food web functioning and stability (Brose et al. 2006, Schneider et al. 2016). However, differences in species body mass only partly reflect species diversity (Brose et al. 2006), and species differences for other traits can affect the relationship between diversity and ecosystem functioning and its stability (Maureaud et al. 2020). One of the most important determinants of diversity that is lacking in our model is probably the diversity in species responses to perturbations, and most importantly environmental fluctuations. In our model, the temporal variability of biomasses only results from intrinsic processes and not from perturbations. Species differences in their response to perturbations have been shown central to our understanding of the diversity–stability relation at community and ecosystem levels, especially as such differences can decrease the synchrony among species (Loreau and de Mazancourt 2008, Griffin et al. 2009, Kéfi et al. 2019, van der Plas 2019, but see Gross et al. 2014, Arnoldi et al. 2019). Thus, we acknowledge that our model is lacking mechanisms that might lead to stronger and more positive effects of diversity on the stability of ecosystem functions. Whether our results are robust to the inclusion of stochastic perturbations remains to be tested. Anyhow, our study brings interesting insights on the deterministic and intrinsic part of stability.

A number of studies have also shown that our understanding of the diversity–stability relationship strongly depends on the stability metric considered, opposite relations arising from different stability metrics (Ives and Carpenter 2007, Pennekamp et al. 2018). Our results add further evidence to this issue in an allometric food web model as we show that the diversity–stability relationship is different when measuring stability as the food web being locally stable (in a stable equilibrium) than when considering the coefficient of variation of total biomasses of unstable webs. Indeed, we found that higher plant and animal richness decrease the probability of observing static total biomass over time, which is fully coherent with classical findings of theoretical ecology in food webs regarding local stability (May 1972, Allesina and Tang 2012).

The relative importance of synchrony versus population stability for the variability of total biomasses

Our results suggest that the variations of the total animal biomass CV among food webs are mostly related to the variations of the mean weighted population CV, while the relative contributions of synchrony and population variability are as expected from the mathematical expression for the total plant biomass CV, synchrony being half as important as population variability for plants. These results contrast with the importance of synchrony for community stability reported by previous studies on plants (Loreau and de Mazancourt 2008, Gross et al. 2014, van der Plas 2019) and several animal trophic groups (Blüthgen et al. 2016, Olivier et al. 2020). Such lower relative importance of synchrony for the stability of total animal biomass in our model might be explained by the complex inter-dependencies within the animal community due not only to competition for resources (as for plants) but also to predatory interactions among animals. Indeed, trophic interactions are known to potentially strongly affect consumer–resource dynamics (McCann and Rooney 2009), and such effects are likely more complex in food webs compared to more simple systems, due to an increase in the number of predatory links. A recent study on the stability of fish food webs also suggested that variations in synchrony might matter less for the temporal stability of animal total biomass than previously observed in plant communities due to the multitrophic structure of these communities (Danet et al. 2021).

These results highlight that understanding the stability of ecosystem functions requires to assess not only the determinants of species synchrony, which has received much attention in this context (Blüthgen et al. 2016, Valencia et al. 2020), but also the determinants of mean weighted population stability. This is even more important given that species richness and mean weighted trophic level often have opposite impacts on these two stability components. For instance, we found that the mean weighted trophic level both strongly stabilised and destabilised total plant biomass CV, by increasing the synchrony among the plant species (destabilising) and reducing the plant populations CV (stabilising) at the same time (Fig. 3). Such type of opposite impacts have been found in plant community experiments (for example, Tilman et al. 2006, Hector et al. 2010) and in a recent food web study (Danet et al. 2021), and it might explain the fair differences in results across the range of studies published on community and ecosystem stability: while many describe a positive diversity–stability relationship, a significant number of them found no relationship or a negative one (Ives and Carpenter 2007, Griffin et al. 2009, Jiang and Pu 2009, Gross et al. 2014, van der Plas 2019). However, studies comparing the relative importance of synchrony and mean weighted population CV for determining variations in community stability are still scarce, making it difficult to conclude about the importance of the populations CV for stability.

Food web structure, total biomass and stability

Our results highlight that the distribution of biomass within food webs is strongly related to the stability of total plant and animal biomasses. Biomass distribution has been emphasized as an important determinant of food web stability in several recent studies (McCauley et al. 2018, Barbier and Loreau 2019). Top-heaviness (i.e. higher consumer to resource biomass ratio) has indeed been related to increased CV of overall total biomass in an allometric food web model (McCauley et al. 2018), with which our results are not coherent, neither for the probability of local stability (stabilising effects of storing biomass at the top of the food web, as seen with the trophic level metric), nor with our stabilising effects of total biomasses and mean weighted trophic level on the CV of total animal biomass of unstable food webs. More work is thus needed on this topic.

However, the positive relation between the mean weighted trophic level and the stability of total biomasses in food webs was also found in a recent empirical study on fish communities in streams (Danet et al. 2021). This effect of mean food web trophic level might be explained by the allometric relations included in our model and present in the ecosystem studied by Danet et al. (2021), where species with larger body mass are positioned at higher trophic levels and are characterized by lower per unit biomass metabolic and attack rates. In such allometric dynamical food web model, species with larger body mass, which have also slower metabolism, are indeed expected to promote food web stability (Brose et al. 2006, Barbier and Loreau 2019). The stabilizing effects of species with larger body mass might also explain the stabilizing effect of plant biomass on the CV of total plant biomass, as plant communities with more biomass tend to have also larger plant species (Fig. 1a).

Contrary to our expectation from literature (May 1972, Allesina and Tang 2012), connectance was not consistently related with stability. Indeed, while connectance was destabilising when looking at the stability probability metric, which was closer to the metric historically used, it had very little impact on the CVs of total biomasses. The absence of relation between connectance and several specific stability measures has been also observed in several food web community matrices parametrised with empirical data (Jacquet et al. 2016) and in stream food webs (Danet et al. 2021). Such absence of connectance effect might result from the non-random distribution of interaction strengths in food webs, which has been shown to result from biomass distribution and allometric constraints, although our measure of connectance was here weighted by feeding rates. Anyhow, we show again here that stability is a multidimensional concept with different measures which can have different behaviours.

Overall, our results thus suggest that the distribution of biomass in food webs strongly matters for the stability of ecosystem functions such as total biomass, meaning that the effects of species richness and food web structure on total biomass are not independent from their effects on the stability of total biomasses (Cardinale et al. 2013, Wang et al. 2021).

Conclusion and perspectives

In summary, our study shows that diversity and mean weighted trophic level not only affect ecosystem functions, as found by recent food web models, but also their temporal stability. We suggest that previously reported BEF relations differ in a food web context, and highlight the need to study the mean weighted population CV at the same time than synchrony to better understand the stability of ecosystems (Xu et al. 2021). One limit of our analysis is that the temporal variability of biomasses only results from intrinsic processes and not from perturbations. Stability is a multidimensional concept, and most of its metrics can be only understood in the light of a perturbation (Donohue et al. 2016, Kéfi et al. 2019), such as resilience or resistance. Thus, future studies will need to investigate how different types of perturbations affect our conclusions on the effects of diversity and food web structure on temporal variability and other measures of the stability of ecosystem functions.

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Author contributions

Jérôme Eschenbrenner: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead). **Élisa Thébault**: Conceptualization (supporting); Funding acquisition (lead); Supervision (lead); Validation (lead); Writing – review and editing (lead).

Data availability statement

Data are available on Zenodo: <https://doi.org/10.5281/zenodo.5081818> (Eschenbrenner and Thébault 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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