

How biotic interactions structure species' responses to perturbations

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Abstract

Predicting how ecological communities will respond to disturbances is notoriously challenging, especially given the variability in species' responses within the same community. Focusing solely on aggregate responses may obscure extinction risks for certain species due to compensatory effects, emphasizing the need to understand the drivers of the response variability at the species-level. Yet, these drivers remain poorly understood. Here, we reveal that despite the typical complexity of biotic interaction networks, species' responses should follow a discernible pattern. Specifically, we demonstrate that the species whose population abundances are most reduced by biotic interactions – which are not always the rarest species – will be those that exhibit the strongest responses to disturbances. This insight enables us to pinpoint sensitive species within communities without requiring precise information about biotic interactions. Our novel approach introduces avenues for future research aimed at identifying sensitive species and elucidating their impacts on entire communities.

Keywords: stability, resilience, reactivity, population dynamics, ecological modelling

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Introduction

Revealing the mechanisms underlying the stability of ecological systems poses a major challenge for ecologists, and one that is becoming ever more pressing with the current biodiversity crisis (Watson et al., 2019). In ecology, stability recovers many meanings (Ives & Carpenter, 2007; Donohue et al., 2013; 2016; Kéfi et al., 2019), reflecting the rich history of the field. In essence, stability seeks to characterize the way a community responds to disturbances. One classic approach is to equate stability with the capacity of a community to revert to its original state after weak disturbances (May, 1973). In this sense, stability centres on the long-term recovery of communities (Arnoldi et al., 2018).

There is a growing recognition, however, that the response of communities to disturbances is multidimensional and thus cannot be reduced to a single stability measure (Donohue et al., 2013; 2016; Pennekamp et al., 2018; Arnoldi et al., 2019; Kéfi et al., 2019). The multidimensional aspect of community responses is, in part, a result of their evolution over time. For example, the short- and long-term response of a community can differ greatly (Arnoldi et al., 2018). More generally, even if a community eventually returns to its original stable state, it can still display a wide variety of behaviours during its transient dynamics (Hastings, 2004; Hastings et al., 2018).

A great body of work has already emphasized the importance of studying transient recovery regimes (Ludwig et al., 1978; Hastings, 2004; Hastings et al., 2018). In ecology (Neubert & Caswell, 1997; Arnoldi et al., 2018), epidemiology (O'Regan et al., 2020) and network science (Asllani et al., 2018; Muolo et al., 2019), a system's transient recovery is often described by its 'reactivity', defined as the system's overall ability to initially amplify perturbations (Neubert & Caswell, 1997). In ecology, (Tang & Allesina, 2014) suggested that reactivity could be used as an early-warning signal of transitions toward instability in complex communities, while (Yang et al., 2023) recently showed, for communities subjected to frequent perturbations, that reactivity is a better predictor than stability of the risk of species extinction. Reactivity is thus a useful alternative to the traditional stability notion, giving a complementary picture of a system's overall response to perturbations.

Yet, reactivity is a system-level concept and, from the perspective of community ecology, overlooks the variability in species individual responses. This means that, due to compensatory dynamics between species, a community may appear weakly affected by a disturbance (e.g. not reactive), while in reality some of its constituent species undergo large variations of their population size, and risk local extinction (Supp & Ernest, 2014). To derive tangible ecological predictions of community recovery, it is thus crucial to understand how responses to perturbations manifest across the biological hierarchy, from populations to communities.

Here, we aim to determine whether and how the variability in species response intensity is structured within communities. Our approach first involves quantifying response intensity, where high intensity should indicate potential nonlinear population dynamics following a pulse perturbation, and a risk of extinction. In theory, recovery dynamics can be studied by linearizing a given dynamical community model in the vicinity of its unperturbed, steady state (Strogatz, 2018). The reliability of this approach hinges on the assumption that all species populations remain 'close' to their unperturbed state immediately after a disturbance, and throughout their recovery. However, even after mild perturbations, species populations can exhibit strong responses and move temporarily 'far' from their unperturbed state. For such responses, the linear approximation is no longer reliable at all times and, in this sense, the recovery of certain species becomes unpredictable, which may in turn undermine the predictability of the recovery of the whole community (Neubert & Caswell, 1997).

In the light of these observations, our theoretical framework seeks to characterize – to then predict – species response intensity in a manner that directly relates to the nonlinearity of species' population dynamics. By doing so, we wish to give a precise meaning to the notion of a species being 'close' or 'far' from its unperturbed state. To summarize, we want to identify sensitive species with a community (and understand how those sensitivities are distributed) where a sensitive species is one whose population either faces a risk of extinction after a perturbation, or tends to exhibit hard-to-predict nonlinear dynamical behaviour during its recovery.

The source of variability in species responses to disturbances is twofold. First, differences in species responses can arise from inherent variations in their life-history strategies, and notably in their generation times and growth rates (Gamelon et al., 2014; Salguero-Gómez et al., 2016; Capdevila et al., 2022). Second, the response of a species within a community can be influenced by its interactions with other species, where the network of these interactions acts as a conduit through which disturbances spread across the community. For example, various studies on food webs have underscored how the hierarchical structure of trophic interactions renders apex predators more susceptible to disturbances (Estes et al., 2011; Beauchesne et al., 2021). However, it remains in general unclear how the variability of species' responses is organised within ecological communities.

Our objective here is to reveal the generic structure in species' responses that biotic interactions induce. To do so, we break down community recovery to the species level, and subsequently reconstruct the recovery of the entire community. Despite the inherent complexity of the network of biotic interactions among species, we show that the variability in species responses exhibits a well-defined structure. This structure reflects the collective impact of biotic interactions on the equilibrium abundances of species.

Specifically, using a minimal Lotka-Volterra model, we uncover that species experiencing greater reductions in their equilibrium abundance due to biotic interactions show stronger responses to disturbances. Next, we emphasize that a species' abundance does not necessarily indicate its sensitivity to perturbations. Finally, we demonstrate that understanding the relationship between species abundance and sensitivity provides valuable insights into the response of the entire community.

Material and methods

Mathematical framework

Quantifying interactions' impact on species equilibrium abundance. When introducing a given species i in a community, its abundance (N_i) will differ from its value (K_i) if species i had been alone in this environment. This abundance change is caused by biotic interactions that directly impacts species i , but also due to the interactions amongst other species, as well as interactions that species i exerts on the community (Arnoldi et al., 2022). Here, we quantify the impact of biotic interactions on a species abundance using the classic notion of relative yield (Loreau & Hector, 2001), denoted $\eta_i = \frac{N_i}{K_i}$, which is the ratio of the species abundance in the community over its carrying capacity (Figure 1 A). The lower a species' relative yield is, the more its equilibrium abundance has been reduced by the effect of biotic interactions.

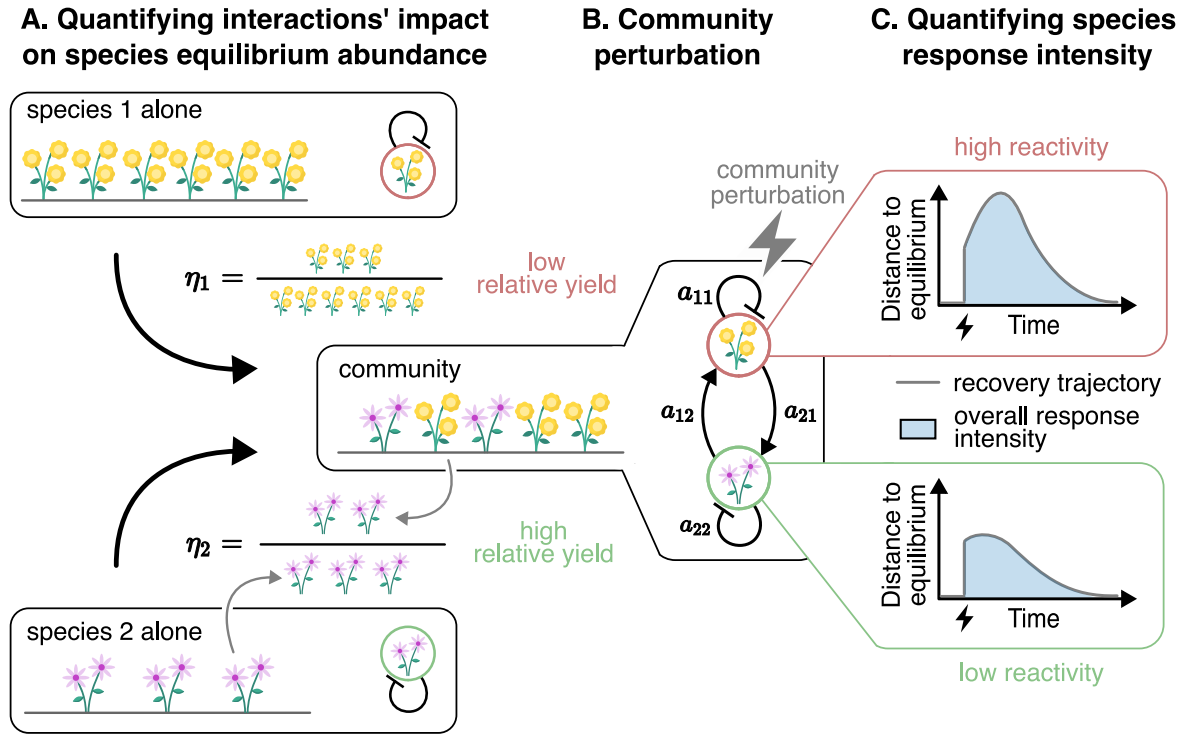


Figure 1 – Visual summary. A) When assembled in a community, species equilibrium abundances can rise or fall because of interactions. We quantify this impact of interactions on species equilibrium abundance with the relative yield of species $\eta_i = \frac{N_i}{K_i}$, with N_i is the species abundance in community, and K_i its carrying capacity. If the interactions' impact is weak, the relative yield is high (i.e. close to or above one). On the contrary, if the impact is high, the relative yield is low. B) Because we are interested in the stability of species and communities, we apply random ‘pulse’ perturbations on the community. C) For each species, we measure its reactivity, that is its ability to amplify the initial perturbation. We use the reactivity as a proxy for the overall species response intensity: we expect that the more reactive the species, the stronger its response to perturbations.

Community model. We consider a community made up of S species, and focus on their relative yields η_i , where $i = 1, \dots, S$ indexes the species (Figure 1 A; see electronic supplementary material section S1 for details). We model the community dynamics with Lotka-Volterra equations

$$\frac{1}{\eta_i} \frac{d\eta_i}{dt} = r_i \left(1 - \eta_i - \sum_{j \neq i} a_{ij} \eta_j \right) \quad (1)$$

The interaction between species i and j is captured by a_{ij} , and the inverse of r_i represents species generation times. For sake of clarity, we assume in the main text that species have equal generation times, and we take $r_i = 1$ (but see electronic supplementary material section S2 where we explain how to release this assumption). Species non-trivial steady states η_i^* are obtained by finding relative yields that cancel the RHS of Eq. 1.

$$\eta_i^* = 1 - \sum_{j \neq i} a_{ij} \eta_j^* \quad (2)$$

Relative deviation from equilibrium. In what follows, we want to investigate how species deviate from their equilibrium to quantify how strongly they respond to perturbations. To do so, we choose to focus on the relative deviation to equilibrium

$$z_i(t) = \frac{\eta_i(t) - \eta_i^*}{\eta_i^*} = \frac{N_i(t) - N_i^*}{N_i^*} \quad (3)$$

We made this decision because, ecologically speaking, it is often relevant to analyse species deviation relative to its steady state value. This is particularly pertinent when studying the risk of extinction, where $z_i(t)$ becomes a crucial variable of interest. Rare species may exhibit minimal absolute variation $|N_i(t) - N_i^*| \ll 1$, yet still be very close to extinction. Conversely, a relative variation approaching -1 (total extinction corresponding to $z_i = -1$) consistently signals species near extinction, regardless of their equilibrium abundance. Moreover, we discuss in the electronic supplementary material section S3 that relative deviation also serves as an indicator of the non-linearity of population dynamics.

Quantifying species' response intensity. A common understanding in dynamical systems is that even a small initial perturbation can undergo substantial amplification, leading to strong responses during transient dynamics. In the context of community dynamics, this phenomenon is typically characterized by the concept of reactivity (Neubert & Caswell, 1997). We extend this conventional notion to the species level, introducing what we term 'species reactivity,' denoted as $R_0^{(i)}$. Species reactivity measures the extent to which a species can amplify an initial perturbation, formally:

$$R_0^{(i)} = \max_{\|z(0)\|=1} \left| \frac{d|z_i|}{dt} \right|_{t=0} \quad (4)$$

To derive a practical and analytically tractable expression for species reactivity, we use a methodology akin to that used for community reactivity. Ultimately, we obtain the following simple expression (see electronic supplementary material section S9 for derivation)

$$R_0^{(i)} = \sqrt{\sum_{j \neq i} (a_{ij} \eta_j^*)^2} \quad (5)$$

The reactivity of a given species is therefore expressed as a weighted sum of the interaction it received, where the weights are the relative yield of its interacting partners (in our case, its direct competitors). Importantly, species reactivity is always positive; that is, for any species, there exists a perturbation that will be initially amplified.

The expression of species reactivity requires a precise knowledge of species interactions, as it depends on the interactions coefficients. However, this knowledge is often lacking in empirical data. To circumvent the need of knowing all pairwise interactions occurring between species, we derive an expectation of species reactivity, that only depends on the mean and variance of pairwise interactions. We provide the full derivation as well as its expression in the electronic supplementary material section S11.

Simulations

Community assembly. We assemble species-rich communities made of $S = 50$ species, with interactions a_{ij} drawn from a truncated normal distribution $a_{ij} \sim |\mathcal{N}(0, \sigma^2)|$ with $\sigma = 0.1$, thus modelling purely competitive communities. Note that we show in the electronic supplementary material section S6 that incorporating a moderate fraction of positive interactions does not substantially alter our results. Moreover, we assume the interaction network to be fully connected, so that all species interact with all others, but our results holds beyond this limit case (see electronic supplementary material section S7 where we consider random partially connected interaction matrices, as well as structured matrices).

Community perturbations. For convenience, we consider that species are, on average, disturbed proportionally to their unperturbed abundance (Arnoldi et al., 2018). In this way we can easily control the initial intensity of the perturbation (again, this assumption is not key for our results, see electronic supplementary material section S5). In terms of relative yields, this amounts to perturbing the latter proportionally to their unperturbed values. To simulate such perturbations, we generate a vector whose coefficients x_i are drawn independently $x_i \sim \mathcal{N}(0, 1)$ and then multiply these coefficients by the corresponding unperturbed relative yields. The amplitude of the perturbations is then set to the arbitrary moderate value: $\sqrt{\langle z_i(0)^2 \rangle_i} = 0.6$.

Response intensity. We expect species reactivity to correlate with the overall response intensity of a species, defined as the integrated response over the whole course of that population's dynamics (Figure 1 C). To test this idea, we first define response intensity at the species-level as

$$R_{sp}(T) = \frac{1}{T} \frac{1}{|z(0)|} \int_0^T |z(t)| dt \quad (6)$$

representing the normalized temporal averaged of $z(t) = \frac{\eta_i(t) - \eta_i^*}{\eta_i^*}$, which is our measure of species non-linearity and risk of extinction. Similarly, we define the response intensity at the community-level as

$$R_{com}(T) = \frac{1}{T} \frac{1}{|\Delta N_{tot}(0)|} \int_0^T |\Delta N_{tot}(t)| dt \quad (7)$$

Where ΔN_{tot} denotes the deviation of total abundance to its equilibrium value. Numerically, we take $T = 1,000$ as the average window.

Selection effect. We also aim to unveil the factors determining the sensitivity of the whole community, using what we have learned at the species-level. To do so, we focus on the notion of 'selection effect', first used in the seminal work of (Loreau & Hector, 2001). The selection effect quantifies the covariance between the relative yield of species (that is, their performance in the community) and their carrying capacity (that is, their performance when alone). Specifically, we want to investigate the impact of the sign of the selection effect on the relationship between the species reactivity and their equilibrium abundance. To achieve this, we consider the three following carrying capacity distributions

$$K_i \sim (1 + \varepsilon_i) \times \eta_i^{*-5/4} \quad (8)$$

$$K_i \sim (1 + \varepsilon_i) \times \eta_i^{*-1} \quad (9)$$

$$K_i \sim (1 + \varepsilon_i) \times \eta_i^* \quad (10)$$

where ε_i is a noise term drawn in $\mathcal{N}(0, 1)$. The first two distributions lead to a negative selection effect, while the last one generates to a positive selection effect. Once species carrying capacities are drawn, we can deduce species equilibrium abundances from their relative yield $N_i^* = \eta_i^* K_i$.

Empirical data

We employ processed data from (Barbier et al., 2021) originating from a grassland biodiversity experiments in Wageningen, Netherlands (Van Ruijven & Berendse, 2009) with eight plant species. The processed data is composed of inferred plant carrying capacities K_i and pairwise interactions a_{ij} . This inference approach produces distributions of the estimated parameters, that are summarized with median (μ), first and last decile (respectively q_{10} and q_{90}).

We drew parameters in normal distributions whose mean $\tilde{\mu}$ and standard deviation $\tilde{\sigma}$ were computed from the estimated parameter distributions. Specifically, the mean was set to the median of the parameter distribution from the data ($\tilde{\mu} = \mu$) and the standard deviation was set so that the inter-decile gap of the distribution from the data equates to the normal distribution inter-decile gap (centred around $\tilde{\mu}$): $\tilde{q}_{90} - \tilde{q}_{10} = q_{90} - q_{10}$, with \tilde{q}_{10} and \tilde{q}_{90} the deciles of the normal distribution. Once the parameters are drawn, we run the dynamics until a stable equilibrium, where at least six species survived, is reached.

To investigate the influence of the sign of the selection effect on the response intensity of communities, we classified communities depending on the sign of their selection effect. We assessed the sign of the selection effect with a correlation test: if the correlation $\text{cor}(\eta_i^*, K_i)$ was not significant ($p > 0.01$), we considered a null selection effect. Otherwise, we considered a negative or positive selection effect, depending on the sign of the correlation.

Results

Stronger responses to perturbations in species most negatively affected by interactions

We derived an analytical measure of species reactivity in Eq. 5, which quantifies the ability of a species to amplify an initial perturbation. Surprisingly, the reactivity of a species depends only on the interactions directed towards it, and not on the interaction of the species with itself. This strong dependence on biotic interactions prompts an examination of how reactivity is influenced by the impact of interactions on equilibrium abundances, quantified here by species relative yields. To investigate this relationship, we plot the reactivity of species against their relative yield in Figure 2 A. As predicted by both of our analytical prediction, we found that the reactivity of species decreases with their relative yield. In ecological terms, species whose abundance is strongly reduced due to biotic interactions amplify perturbations to a greater extent.

Furthermore, our results demonstrate that our analytical prediction accurately captures how the reactivity of species is shaped by their relative yields. Remarkably, our prediction achieves this using only general information about the distribution of interactions (mean and variance). In other words, we are able to unveil the relationship between the net impact of interactions – measured by the rel-

active yield – and the total intensity of direct interactions that govern species reactivity. The latter represents the impact of both positive and negative interactions through direct and indirect pathways, while the former focuses exclusively on the absolute value of direct interactions. We show how sensitive this relationship is to the inclusion of positive interactions in Section S6 of the electronic supplementary material.

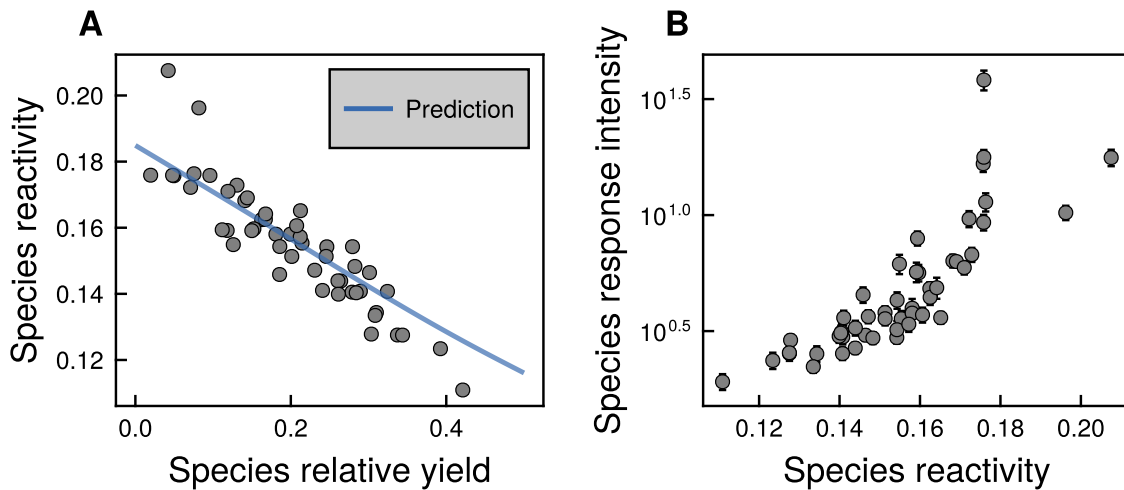


Figure 2 – Species whose abundance is most reduced by biotic interactions exhibit stronger responses to perturbations. A) The reactivity of species (their worst-case initial response to pulse-perturbations) against their relative yield, which quantifies the impact of biotic interactions on species' equilibrium abundance. The solid line corresponds to theoretical expectation of species reactivity (see electronic supporting materials section S11 for details). B) Overall response intensity of species recovery against their reactivity. Simulations are performed for a single community. Species' overall response intensity is averaged over 100 random perturbations. Error bars correspond to standard error.

We anticipate that species reactivity, while assessing a species' short-term response to perturbations, should also determine, at least to some extent, the overall response of the species, along its entire recovery dynamics, and following various perturbations. To validate that expectation, we quantify a species' overall response intensity (Figure 1 C) and plot it against species reactivity (Figure 2 B). As expected, we observe that species reactivity serves as a reliable proxy to assess the species' overall response intensity to perturbations. Therefore, we can confidently use a species' reactivity to quantify how strongly it will tend to respond to disturbances. Furthermore, we note that species relative yield, because it directly correlates with species reactivity and resilience is, *de facto*, also a strong predictor of species overall response intensity (see electronic supplementary material section S8). Finally, we confirm that stronger species responses are harder to predict with the linear approximation (see electronic supplementary material section S4).

In sum, these results indicate that a species' relative yield determines the intensity of that species responses to perturbations. However, unlike species abundances, relative yields are often unavailable in data, as species carrying capacities are typically unobserved. Therefore, we will now establish a relationship between species reactivity.

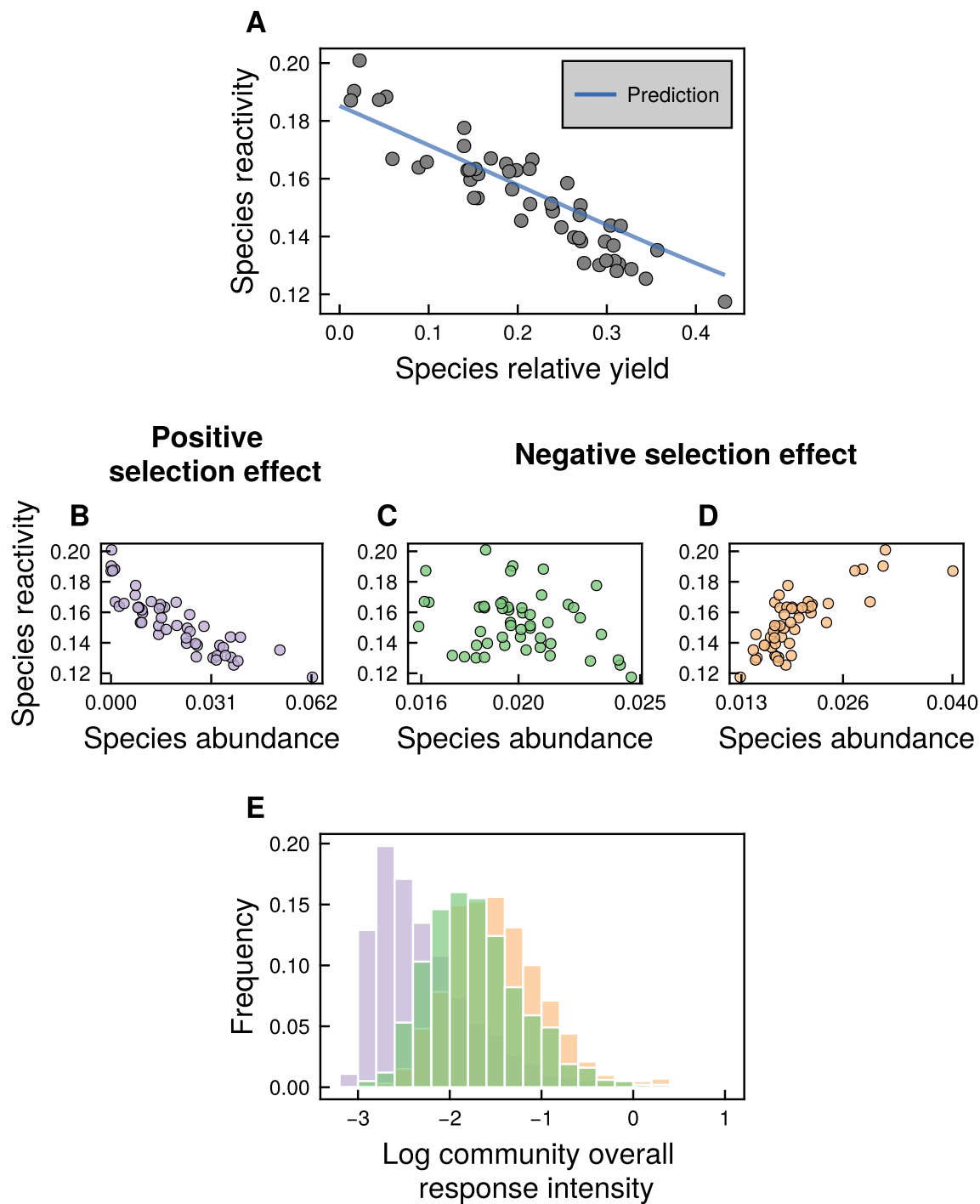


Figure 3 – Selection effect indicates how strongly communities respond to perturbations. A) The reactivity of species against their relative yield for a single community. The blue solid line corresponds to the theoretical full expectation (see Material and methods). B-D) The same species reactivity-relative yield relationship can correspond to many species reactivity-abundance relationships. This mapping from one-to-many is determined by the selection effect. For the given reactivity-relative yield relationship, we illustrate that we can observe a negative reactivity-abundance relationship if the selection effect is positive (B), or a null or positive one if the selection effect is positive (C, D). E) Consequences of the reactivity-abundance relationship on the community overall response intensity. Colours correspond to colours of the reactivity-abundance relationship (B-D).

Response intensity at the community-level depends on selection effects during assembly

We can now unveil the missing link between the reactivity of species and their abundance using the ‘selection effect’ concept of (Loreau & Hector, 2001). The selection effect quantifies how species features when alone (*i.e.*, their carrying capacity) relate to their performance in multi-species communities (*i.e.*, their relative yield). A positive selection effect occurs when species with the best feature perform best in the community, whereas a negative selection corresponds to the opposite phenomenon. Crucially, species relative yields and abundances are not necessarily positively correlated, so that a rare species in the community can be abundant alone and conversely.

As a result, we illustrate in Figure 3 that for a given species reactivity-relative yield relationship (Figure 3 A), we can observe different species reactivity-abundance relationships depending on the sign of the selection effect (Figure 3 B-D). More specifically, we show that a positive selection effect leads to a decrease in species reactivity with their abundance (Figure 3 B), while a negative selection effect leads to a null or positive trend between reactivity and abundance (Figure 3 C, D). We anticipate that the sign of the reactivity-abundance relationship impacts the response of the whole community. Indeed, we anticipate weak community responses if the most abundant species are the least reactive, and on the contrary, we expect strong community responses if the most abundant species are also the most reactive.

To test this claim, we can draw the distribution of community response intensities for the three abundance-reactivity relationships previously investigated: negative, null or positive (Figure 3 D). As anticipated, the community with a negative selection effect exhibits stronger responses to perturbations than the community with a positive selection effect.

So far, we have explored different scenarios for the reactivity-abundance relationship, corresponding to variations in the sign of the selection effect, and their consequences for community-level responses to perturbations. Next, we investigate these relationships in empirical data from a plant community.

Case-study: communities parameterized using data from a grassland experiment

We assemble a set of communities using interactions and carrying capacities extracted from empirical data of a plant community (*cf.* Material and methods). We can first plot the reactivity of species against their relative yield (Figure 4 A). Notably, we observe a consistent decrease in species reactivity with their relative yield, mirroring the pattern observed in randomly parameterized communities (Figure 2 A). We find that our theoretical expectation of species reactivity closely aligns with the observed data (solid lines in Figure 4 A), despite being based on assumptions that may not hold true in natural communities (such as supposing *i.i.d* normally distributed interactions strength between species).

Next, we examine the relationship between species reactivity and their abundance in communities displaying a positive selection effect (Figure 4 B) and a negative one (Figure 4 C). As expected, we observe a decrease of species reactivity with their abundance in communities with a positive selection. Conversely, for communities with a negative selection, we find no significant trend between species reactivity and abundance, akin to the pattern observed in Figure 3 C. Consistent with our findings in randomly parameterized communities, we anticipate that the relationship between species reactivity and abundance influences the response of the entire community.

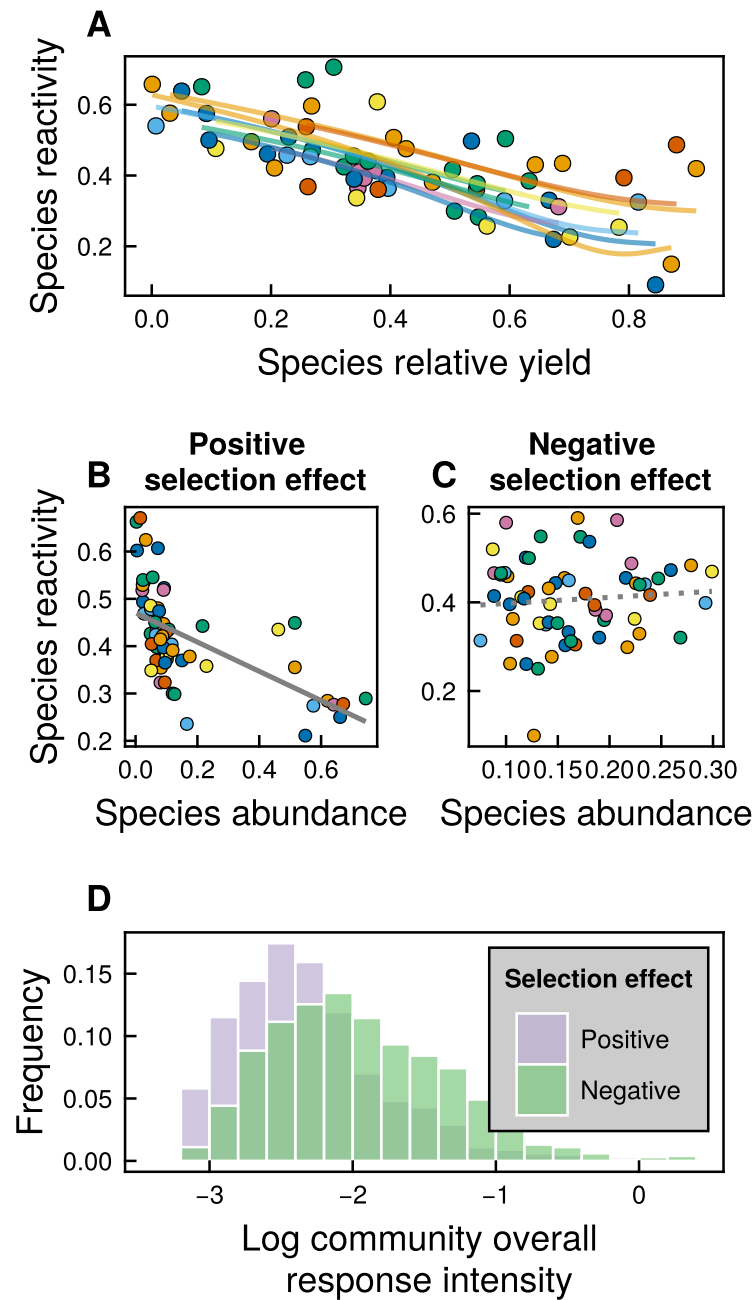


Figure 4 – The structure of the variability in species response intensity inform on the responses of communities parameterized from grassland community data. A) The reactivity of species against their relative yield for 10 communities parameterized using empirical data. Each colour corresponds to one community. Solid lines correspond to the full theoretical expectation of species reactivity for each community. B-C) The reactivity of species against their abundance for 10 communities respectively with a positive selection effect (B) and a negative one (C). Grey lines correspond to a linear fit which is solid if the trend is significant ($p < 0.05$) and dashed otherwise. C) Community overall response intensity, depending on the sign of the selection effect occurring in the community. On the two set of communities previously generated (positive and negative selection effect), we applied 100 random perturbations on each community.

We may then investigate how the selection effect influences the response intensity of the entire community. We thus extracted the distribution of community response intensities separately for commu-

nities exhibiting positive and negative selection effects (Figure 4 C). The results align with the findings shown in Figure 3 E, demonstrating that communities with a negative selection effect respond more strongly to perturbations compared to those with a positive selection effect.

Discussion

Modern ecology faces the challenge of understanding and predicting the responses of species-rich communities to external disturbances. To build theories and deduce hypothesis, a common strategy is to model communities as complex dynamical systems and view perturbations as deviations from an equilibrium (May, 1973). However, when applying dynamical systems' theory to community models, the response to a disturbance is typically assessed at the system level, overlooking the considerable variability in individual species' responses, and even concealing it when compensatory effects occur (Supp & Ernest, 2014). Our theoretical approach breaks down community responses to the species level, shedding light on how the intensity of species' responses is organized. This, in turn, allows us to make novel predictions regarding whole community responses.

We find, in generic models, that species whose abundances are most reduced by biotic interactions tend to be those that will exhibit the strongest and least predictable response to a given disturbance. This claim is not just an observed correlation; we unveil a precise mapping from the impact of biotic interactions on species' equilibrium abundances to the intensity of their response to disturbances. This mapping, tested on models parameterized with data from grassland experiments, only depends on basic summary statistics of the set of biotic interactions. In essence, we have developed a method for identifying sensitive species in ecological communities without needing detailed information about species interactions.

The unpredictability of sensitive species

In theoretical work, such as ours, stability is often studied by 'linearizing' a given model (Grimm et al., 1992; Kéfi et al., 2019) in the vicinity of an equilibrium point. This approach unlocks powerful mathematical tools, in particular for quantifying the asymptotic recovery of species or of the whole community, regardless of what the disturbance may be.

The reliability of the linear approximation hinges on the assumption that species remain 'close' to their equilibrium throughout their recovery. While this assumption is commonly made in theoretical works, our findings reveal that even mild interactions between species can cause them to exhibit reactive behaviour during their transient recovery, venturing 'far' from their equilibrium. Rather than viewing this observation as a theoretical limitation, we leveraged it to define, while still benefiting from the convenient tools of linear algebra, a concept of 'species reactivity' that directly relate to the potentiality for nonlinear population dynamics. Our analysis has led us to propose that species experiencing the greatest reductions in abundance due to biotic interactions exhibit heightened responses to perturbations, and are likely to manifest transient responses that are hard to predict.

Beyond individual species: unveiling community responses to disturbances

Across communities, species exhibiting the strongest responses to disturbances may vary in their relative abundance. Some communities could feature these species as the most abundant, while in others, they could be the rarest species. Our study reveals that this relationship between species' sensitivities to perturbations and their relative abundance is driven by the sign of the 'selection ef-

fect' characterizing a community's assembly pattern (Loreau & Hector, 2001). Specifically, when the selection effect is negative, the most reactive species also tend to be the most abundant. Given that abundant species contribute the most to total community abundance (or any other broad ecosystem function), we deduce that negative selection effects ought to be associated with stronger community-level responses to perturbations.

This result raises two basic questions: 1) can we evaluate the selection effect using limited data? and 2) how common are communities with negative selection effects in nature? First, previous work has shown that the selection effect can be estimated from a random sample of the community containing more than half of the species (Clark et al., 2019). In addition, information on the community's environment variables may help to estimate the selection effect (Zhang et al., 2021), although studies in this direction remain nascent. Second, the seminal study of (Loreau & Hector, 2001), reported both positive and negative selection effects in several communities. More recently, (Feng et al., 2022) observed negative selection effects in species rich forest plantations. Overall, communities with negative selection effects are thus commonly observed (Cardinale et al., 2011), indicating that it might be commonplace for natural communities to harbour reactive, abundant species.

Differentiating between community and species reactivity

The concept of 'species reactivity' developed here differs from the notion of 'system reactivity' (Neubert & Caswell, 1997) commonly used in ecology (Tang & Allesina, 2014; Kéfi et al., 2019; Yang et al., 2023). These two concepts address distinct levels of biological organization: system reactivity assesses the collective community's capacity to amplify initial perturbations, while species reactivity evaluates this ability within individual species.

This disparity in observation scales underscores significant ecological implications. Community reactivity necessitates a specific structure of biotic interactions to occur (Trefethen, 2005; Asllani et al., 2018; MacKay et al., 2020), whereas species reactivity inherently exists as long as species interact with others. Consequently, species reactivity could be a common feature in ecological communities, while community reactivity is likely less common (but see (MacKay et al., 2020)). The latter can be understood as community reactivity reflects a specific collective behaviour reliant on a specific arrangement of species dynamics.

Revisiting the 'core vs satellite species' dichotomy

From a historical standpoint, our work can be seen as a formalization of the early conjecture of (Caswell, 1978): 'Perhaps a community consists of a core of dominant species, which interact strongly enough among themselves to arrive at equilibrium, surrounded by a larger set of non-equilibrium species playing their roles against the background of the equilibrium species'. This idea was further elaborated upon by Ilkka Hanski in his seminal paper (Hanski, 1982), where he categorized species into 'core' species and 'satellite' species. In the context of our study, 'dominant' or 'core' species align with those exhibiting a high relative yield – indicating minimal impact from biotic interactions on their abundance. Conversely, 'background' or 'satellite' species correspond to those with low relative yield (Arnoldi et al., 2018).

Indeed, the notion of species reactivity precisely captures the tendency of species to remain out of their equilibrium. Then, consistent with Caswell's conjecture, we find that 'dominant' species re-

main close to their equilibrium, exhibiting low reactivity. In contrast, ‘background’ species demonstrate high reactivity, suggesting prolonged transient recovery periods.

Interaction network and species’ responses to disturbances: a two-way relationship

We pinpoint sensitive species within ecological communities by quantifying the relative decrease in their equilibrium abundances due to biotic interactions. This finding begs the question of how to practically gauge this impact to effectively identify sensitive species. In our analysis, we compare species’ equilibrium abundances in isolation versus within a community using the concept of relative yield. However, the notion of relative yield has two main limitations. First, it necessitates knowledge of species’ isolated abundances, which is typically unavailable in empirical datasets. Second, it is not well-defined for species that rely on other species to survive, like herbivores or predators.

Regarding the latter limitation, it is important that the fundamental aspect represented by the relative yield is the departure, caused by inter-specific interactions, from a characteristic density. For species that can grow alone, this density is the ratio of intrinsic growth rate over intra-specific interactions, giving the classic notion of carrying capacity. This characteristic density can be generalized to consumer species (Galiana et al., 2021) as the ratio of mortality over intra-specific competition (or self-regulation). This leads us back to the initial issue of measuring relative yield: estimating population self-regulation could substitute to assessing equilibrium abundances in isolation. Despite these considerations, however, few empirical studies actually offer direct assessments of population self-regulation (Skalski & Gilliam, 2001; Galiana et al., 2021).

Although it may appear that we have reached a dead end, this may suggest turning the problem on its head. Indeed, our work demonstrates that species’ relative yields precisely correspond to the intensity of their responses to disturbances, suggesting a general bidirectional relationship. Therefore, it may be feasible to infer information about species’ relative yields and, consequently, the interactions between species (Bunin, 2017; Barbier et al., 2021) by measuring their responses to perturbations. Essentially, our work suggests that analysing species’ responses to disturbances is a should provide insights about the interaction network of the studied community, which is otherwise notoriously challenging to measure (Carrara et al., 2015).

Contributions

IL, JFA and SK designed the study. IL and JFA developed and analysed the model. IL performed the simulations and wrote the first draft of the manuscript, JFA and SK contributed substantially to revisions.

Code availability

Our code is publicly available at <https://github.com/ismael-lajaaiti/species-reactivity>.

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References

- Arnoldi J-F, Bideault A, Loreau M, Haegeman B (2018) How ecosystems recover from pulse perturbations: A theory of short-to long-term responses. *Journal of theoretical biology*, **436**, 79–92.
- Arnoldi J-F, Barbier M, Kelly R, Barabás G, Jackson A L (2022) Invasions of ecological communities: Hints of impacts in the invader's growth rate. *Methods in Ecology and Evolution*, **13**, 167–182.
- Arnoldi J-F, Loreau M, Haegeman B (2019) The inherent multidimensionality of temporal variability: how common and rare species shape stability patterns. *Ecology letters*, **22**, 1557–1567.
- Asllani M, Lambiotte R, Carletti T (2018) Structure and dynamical behavior of non-normal networks. *Science advances*, **4**, eaau9403.
- Barbier M, De Mazancourt C, Loreau M, Bunin G (2021) Fingerprints of high-dimensional coexistence in complex ecosystems. *Physical Review X*, **11**, 11009–11010.
- Beauchesne D, Cazelles K, Archambault P, Dee L E, Gravel D (2021) On the sensitivity of food webs to multiple stressors. *Ecology Letters*, **24**, 2219–2237.
- Bunin G (2017) Ecological communities with Lotka-Volterra dynamics. *Physical Review E*, **95**, 42414–42415.
- Capdevila P, Stott I, Cant J, Beger M, Rowlands G, Grace M, Salguero-Gómez R (2022) Life history mediates the trade-offs among different components of demographic resilience. *Ecology Letters*, **25**, 1566–1579.
- Cardinale B J, Matulich K L, Hooper D U, Byrnes J E, Duffy E, Gamfeldt L, Balvanera P, O'connor M I, Gonzalez A (2011) The functional role of producer diversity in ecosystems. *American journal of botany*, **98**, 572–592.
- Carrara F, Giometto A, Seymour M, Rinaldo A, Altermatt F (2015) Inferring species interactions in ecological communities: a comparison of methods at different levels of complexity. *Methods in Ecology and Evolution*, **6**, 895–906.
- Caswell H (1978) Predator-mediated coexistence: a nonequilibrium model. *The American Naturalist*, **112**, 127–154.
- Clark A T, Barry K E, Roscher C, Buchmann T, Loreau M, Harpole W S (2019) How to estimate complementarity and selection effects from an incomplete sample of species. *Methods in ecology and evolution*, **10**, 2141–2152.
- Donohue I, Hillebrand H, Montoya J M, Petchey O L, Pimm S L, Fowler M S, Healy K, Jackson A L, Lurgi M, McClean D, others (2016) Navigating the complexity of ecological stability. *Ecology letters*, **19**, 1172–1185.
- Donohue I, Petchey O L, Montoya J M, Jackson A L, McNally L, Viana M, Healy K, Lurgi M, O'Connor N E, Emmerson M C (2013) On the dimensionality of ecological stability. *Ecology letters*, **16**, 421–429.
- Estes J A, Terborgh J, Brashares J S, Power M E, Berger J, Bond W J, Carpenter S R, Essington T E, Holt R D, Jackson J B, others (2011) Trophic downgrading of planet Earth. *science*, **333**, 301–306.
- Feng Y, Schmid B, Loreau M, Forrester D I, Fei S, Zhu J, Tang Z, Zhu J, Hong P, Ji C, others (2022) Multispecies forest plantations outyield monocultures across a broad range of conditions. *Science*, **376**, 865–868.
- Galiana N, Arnoldi J-F, Barbier M, Acloque A, Mazancourt C de, Loreau M (2021) Can biomass distribution across trophic levels predict trophic cascades?. *Ecology Letters*, **24**, 464–476.

- Gamelon M, Gimenez O, Baubet E, Coulson T, Tuljapurkar S, Gaillard J-M (2014) Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. *The American Naturalist*, **184**, 673–683.
- Grimm V, Schmidt E, Wissel C (1992) On the application of stability concepts in ecology. *Ecological modelling*, **63**, 143–161.
- Hanski I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 210–221.
- Hastings A (2004) Transients: the key to long-term ecological understanding?. *Trends in ecology & evolution*, **19**, 39–45.
- Hastings A, Abbott K C, Cuddington K, Francis T, Gellner G, Lai Y-C, Morozov A, Petrovskii S, Scranton K, Zeeman M L (2018) Transient phenomena in ecology. *Science*, **361**, eaat6412.
- Ives A R, Carpenter S R (2007) Stability and diversity of ecosystems. *science*, **317**, 58–62.
- Kéfi S, Dominguez-Garcia V, Donohue I, Fontaine C, Thébault E, Dakos V (2019) Advancing our understanding of ecological stability. *Ecology Letters*, **22**, 1349–1356.
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.
- Ludwig D, Jones D D, Holling C S, others (1978) Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *Journal of animal ecology*, **47**, 315–332.
- MacKay R S, Johnson S, Sansom B (2020) How directed is a directed network?. *Royal Society open science*, **7**, 201138–201139.
- May R M (1973) *Stability and complexity in model ecosystems*. Princeton university press.
- Muolo R, Asllani M, Fanelli D, Maini P K, Carletti T (2019) Patterns of non-normality in networked systems. *Journal of theoretical biology*, **480**, 81–91.
- Neubert M G, Caswell H (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology*, **78**, 653–665.
- O'Regan S M, O'Dea E B, Rohani P, Drake J M (2020) Transient indicators of tipping points in infectious diseases. *Journal of the Royal Society Interface*, **17**, 20200094–20200095.
- Pennekamp F, Pontarp M, Tabi A, Altermatt F, Alther R, Choffat Y, Fronhofer E A, Ganesanandamoorthy P, Garnier A, Griffiths J I, others (2018) Biodiversity increases and decreases ecosystem stability. *Nature*, **563**, 109–112.
- Van Ruijven J, Berendse F (2009) Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, **118**, 101–106.
- Salguero-Gómez R, Jones O R, Jongejans E, Blomberg S P, Hodgson D J, Mbeau-Ache C, Zuidema P A, De Kroon H, Buckley Y M (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, **113**, 230–235.
- Skalski G T, Gilliam J F (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, **82**, 3083–3092.
- Strogatz S H (2018) *Nonlinear dynamics and chaos with student solutions manual: With applications to physics, biology, chemistry, and engineering*. CRC press.
- Supp S R, Ernest S M (2014) Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology*, **95**, 1717–1723.
- Tang S, Allesina S (2014) Reactivity and stability of large ecosystems. *Frontiers in Ecology and Evolution*, **2**, 21–22.

- Trefethen L N (2005) Spectra and Pseudospectra: The Behaviour of Non-normal Matrices and Operators. *The graduate student's guide to numerical analysis' 98: Lecture notes from the VIII EPSRC Summer School in Numerical Analysis*, 217–250.
- Watson R, Baste I, Larigauderie A, Leadley P, Pascual U, Baptiste B, Demissew S, Dziba L, Erpul G, Fazel A, others (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *IPBES Secretariat: Bonn, Germany*, 22–47.
- Yang Y, Coyte K Z, Foster K R, Li A (2023) Reactivity of complex communities can be more important than stability. *Nature Communications*, **14**, 7204–7205.
- Zhang W-P, Gao S-N, Li Z-X, Xu H-S, Yang H, Yang X, Fan H-X, Su Y, Fornara D, Li L (2021) Shifts from complementarity to selection effects maintain high productivity in maize/legume intercropping systems. *Journal of Applied Ecology*, **58**, 2603–2613.

Supplementary Material

How biotic interactions structure species' responses to perturbations

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Code available at: <https://github.com/ismael-lajaaïti/species-reactivity>

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S1. Why relative yield is the relevant parameterization

In our study, we aim to explore how biotic interactions influence species responses to perturbations. To achieve this, it is pertinent to parameterize our system with a variable that quantifies the impact of interaction on species. This impact on species abundances is precisely captured by the concept of relative yield, defined as the species abundance in the community relative to its carrying capacity ($\frac{N_i}{K_i}$) (Loreau, 2010). Our findings support this claim, demonstrating that the relative yield (rather than species abundance) of a species strongly predicts its response intensity to a perturbation.

Furthermore, it is worth noting that the parameterization of relative yield has previously been utilized to investigate species coexistence and interactions between species (Barbier et al., 2021; Carrara et al., 2015). Finally, we have chosen to adhere to the term 'relative yield,' as used in the Biodiversity-Ecosystem-Functioning literature, as we demonstrate that the concept of 'selection effect' – also coined in this literature (Loreau and Hector, 2001) – is pertinent for discussing our results (see figure 2 in the main text).

Below, we explain how to go from the common parameterization to the relative yield parameterization presented in the main text. We start from

$$(S1) \quad \frac{1}{N_i} \frac{dN_i}{dt} = r_i \left(1 - \frac{N_i + \sum_{j \neq i} a'_{ij} N_j}{K_i} \right)$$

If we replace N_i by $\eta_i K_i$, we have

$$(S2) \quad \frac{1}{\eta_i} \frac{d\eta_i}{dt} = r_i \left(1 - \eta_i - \sum_{j \neq i} (a'_{ij} \frac{K_j}{K_i}) \eta_j \right)$$

Then, if we note $a_{ij} = a'_{ij} \frac{K_j}{K_i}$, we recover the equation (1) of the main text. Moreover, note that (Barbier et al., 2021) found out that the interaction of the relative yield interactions (a_{ij}) did not display a strong discernible pattern in natural plant communities, which supports our approach of drawing these interactions randomly (before the assembly process occurs).

S2. Treating species with different timescales

In the main text, we assumed for the sake of simplicity and clarity that all species had the same timescale, defined by their generation time (r_i^{-1}), which was set to unity for all species. However, this assumption is somewhat unrealistic, considering that species with vastly different generation times can coexist within the same community. Therefore, in this section, we release the aforementioned assumption and detail how our framework would apply to species with different generation times.

Our study aims to capture how biotic interactions modulate the species response to disturbance. However, species responses to perturbation are also strongly determined by their generation times. We expect that species with low generation time ('slow species') take a long time to recover, whereas species with a high generation time ('fast species') recover quickly. Therefore, we have to disentangle the effect of biotic interactions and species generation times on their response. To do so, we measure species responses in their relative time $t_i = r_i t$. This scaling allows us to fairly compare slow and fast species, and thereby isolate the effect of biotic interaction on species responses.

Without scaling. If species response is not normalized by its generation time, species reactivity is (derived from equation S12) $\tilde{R}_0^{(i)} = r_i \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$; and the species overall response intensity $\tilde{R}_{sp}^{(i)} = \frac{1}{T} \int_0^T |z_i(t)| dt$. Specifically, we observe that species reactivity is directly proportional to the inverse of generation time, which make slow species less reactive and fast species more reactive. By contrary, we expect the response intensity of slow species to be larger than the response of fast species because their intrinsic return rate is smaller. In sum, we anticipate no clear relationship between reactivity of species and their response intensity without scaling.

With scaling. Species reactivity is $R_0^{(i)} = \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$ (see equation S13). We can note that species reactivity is independent of species generation time, as we expect. Moreover, species overall response intensity becomes: $R_{sp}^{(i)} = r_i \frac{1}{T} \int_0^T |z_i(t)| dt$, because we scale the integration time by r_i . That is, if $r_i \leq 1$ (slow species), we contract integration time. Conversely, if $r_i \geq 1$ (fast species), we dilate integration time.

We propose to investigate the relationship between the reactivity of species and their overall response intensity in a community made up of 50 species. Species growth rates are drawn in $r_i \sim \mathcal{U}(0.1, 1)$. The rest of the community parameters are taken as described in the Material and Methods of the main text.

In figure S1, we investigate how reactivity relates to the species response intensity with and without scaling. We observe that this relationship becomes relevant only if species responses are investigated relatively to their generation time. Indeed, otherwise species reactivity is strongly

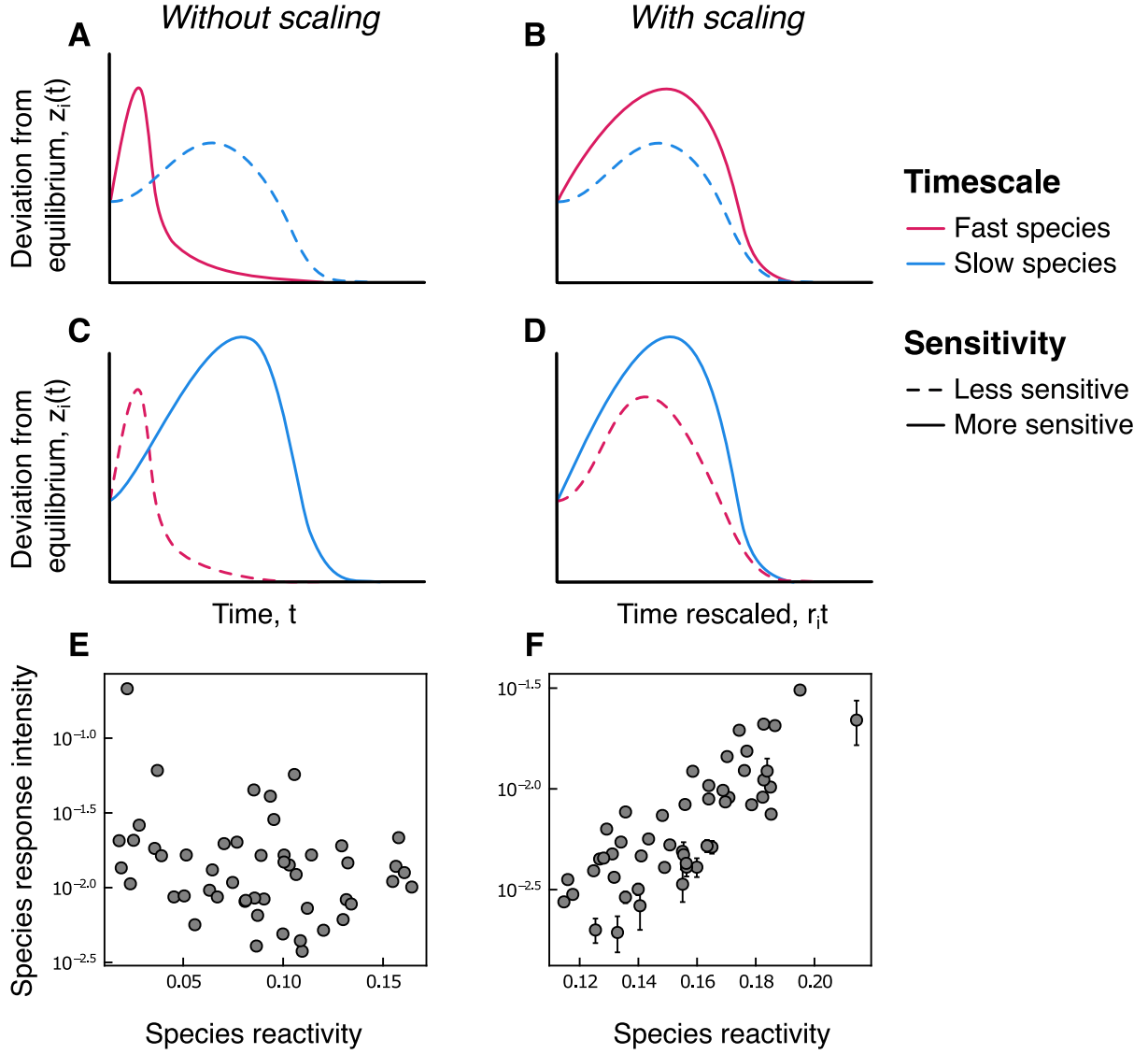


Figure S1 – How to compare responses of species with different generation times. Without scaling, regardless of whether slow species exhibit weaker or stronger responses due to biotic interactions (respectively A and B), their response – defined by the integral of $z_i(t)$ – will appear stronger because it is heavily biased by their generation time (r_i). On the contrary, the reactivity of slow species will often be smaller than that of fast species, as $\tilde{R}_0^{(i)} = r_i \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$. Consequently, we observe no discernible relationship between species reactivity and their response intensity (E). Scaling time, transforming t to $r_i t$, helps alleviate this bias and enables fair comparison of species with different generation times. Indeed, as observed in B and D, when time is rescaled, species reactivity correlates well with species response intensity, as confirmed in F.

biased by the generation time of species, and thereby fail to represent accurately their overall response.

S3. Relative deviation to equilibrium as an indicator of nonlinearity

We show here that the relative deviation to equilibrium ($z_i(t)$) can be used to pinpoint the limit of the linear approximation. The species deviation from equilibrium ($x_i = \eta_i - \eta_i^*$) follows the dynamics (see equation S8)

$$(S3) \quad \frac{dx_i}{dt_i} = - \underbrace{\eta_i^* (x_i + \sum_{j \neq i} a_{ij} x_j)}_{\text{linear}} - \underbrace{x_i (x_i + \sum_{j \neq i} a_{ij} x_j)}_{\text{nonlinear}}$$

The linear approximation assumes that the initial perturbation is small, implying that species deviations remain small throughout the recovery dynamics. Consequently, the nonlinear term on the RHS of equation S3 can be neglected. However, as highlighted by (Neubert and Caswell, 1997), even if the initial perturbation is small (which is not always the case in natural contexts), species deviation can increase substantially during transient dynamics, rendering the linear approximation inapplicable (Trefethen, 2005). Below, we elucidate how the relative deviation precisely captures such phenomena.

The RHS of equation S3 is the sum of a linear term (in x_i) and non-linear one. We note that non-linear dynamics can only be neglected if $|x_i(t)| < \eta_i^*$. If we define $z_i(t) = x_i(t)/\eta_i^*$, this condition simply becomes $|z_i(t)| < 1$. Therefore, we can see $|z_i(t)|$ as a measure of the non-linearity of species i 's dynamics. In the next section, we demonstrate that this measure of nonlinearity indicate how well species recovery trajectories can be predicted by the linear approximation.

S4. Predictability of species' response to perturbations

We expect most reactive species to exhibit a stronger response to pulse perturbations. Here, we decided to quantify the intensity of the species' responses in a manner that directly relates to the nonlinearity of population dynamics. Therefore, we expect in addition that most reactive species are less predictable by the linear approximation, as they tend to move 'far' from their equilibrium.

To check that latter expectation, we first need to quantify the 'predictability' of a species' recovery trajectory. To do so, we compare the trajectory produced by the complete model to the trajectory estimated by the linear approximation. Specifically, the deviation to linearity of species i trajectory is defined as

$$(S4) \quad \Delta_i = \frac{\int_{\mathbb{R}^+} |z_i(t) - \hat{z}_i(t)| dt}{\int_{\mathbb{R}^+} |z_i(t)| dt}$$

Where $z_i(t)$ is the true (algebraic) nonlinearity of species i at time t and $\hat{z}_i(t)$ the value predicted by the linear approximation. Δ_i can be interpreted as the error due to the linear approximation integrated over time. We then quantify the predictability of the trajectory of species i as

$$(S5) \quad \rho_i = e^{-\Delta_i}$$

Thus, predictability spans between zero and one. A predictability of one corresponds to a null error, and decreases toward zero as the error of the linear approximation increases. The notion of predictability is illustrated in figure 1-C. To produce a measure capturing the generic behaviour of species responses to disturbances, we average the species predictability over many recovery trajectories, each obtained by applying a random perturbation.

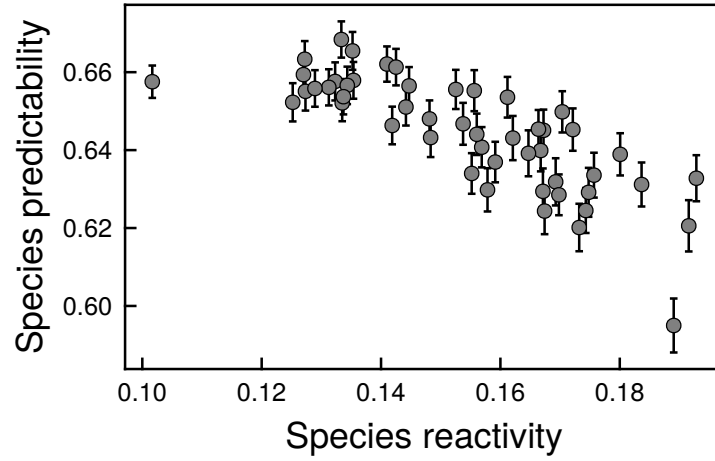


Figure S2 – Species’ responses to perturbations becomes increasingly harder-to-predict, as species becomes more reactive. We assembled a community of $S = 50$ as described in the Material and Methods (Main text) and plotted the reactivity of species against their predictability. Species predictability is averaged over 1,000 random perturbations. Error bars correspond to standard error.

S5. Exploring different types of perturbations

In the main text, we consider perturbations that are, on average, proportional to species’ relative yield. However, this assumption is not necessary for our results to hold. In figure S3, we illustrate the relationship between species reactivity and their response intensity for three types of perturbations: proportional perturbations, equal perturbations (where all species are, on average, perturbed equally), and inversely proportional perturbations (where species are, on average, perturbed inversely proportionally to their relative yield). We observe that for all three types of perturbations considered, species reactivity accurately predicts species response intensity. Lastly, please note that we do not depict the relationship between species’ relative yield and their reactivity, as both reactivity and yield do not explicitly depend on the type of perturbation.

S6. Incorporating positive interactions

We primarily use our framework to explore competitive plant communities. However, it is relevant to note that interactions between species do not necessarily have to be strictly negative for our results to remain valid. As demonstrated in figure S4, as long as the fraction of positive interactions remains moderate, our predictions remain effective.

However, as the fraction of positive interactions increases, we observe that the relative yield of species predicts their reactivity less accurately. This discrepancy arises because the clear negative trend observed between species reactivity and relative yield in purely competitive communities is primarily due to species with lower relative yield receiving more squared interactions (a_{ij}^2), as depicted in Figure S7-B. Intuitively, this implies that species experiencing greater reductions in abundance also experience more competitive interactions. However, when positive interactions are introduced, we do not expect this negative relationship between squared received interactions and relative yield to hold, because conversely, species abundance benefits from stronger (positive) interactions. In sum, we believe that the addition of positive interactions dissipates

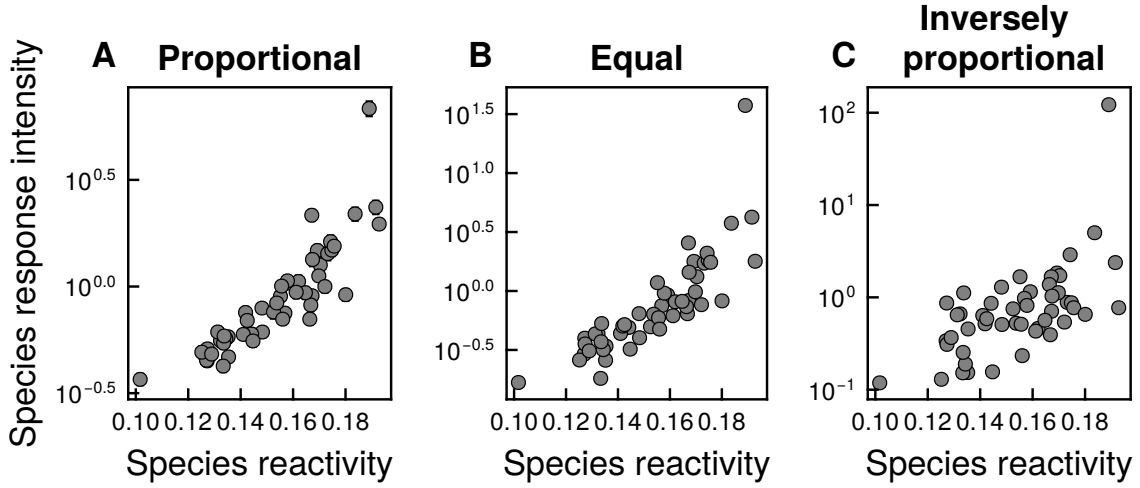


Figure S3 – Response intensity of species against their reactivity for different types of perturbations. A) Proportional perturbations, the perturbation on species i is drawn in $x_i \sim \eta_i \mathcal{N}(0, 1)$ (before normalization). B) Equal perturbations, the perturbation on species i is drawn in $x_i \sim \mathcal{N}(0, 1)$. C) Inversely proportional perturbations, the perturbation on species i is drawn in $x_i \sim \frac{1}{\eta_i} \mathcal{N}(0, 1)$. For all perturbation types, the perturbation vector \mathbf{x} is normalized such that the total relative deviation of the community at $t = 0$ is equal to $\|\mathbf{z}(0)\| = 1$. The latter ensures the fair comparison between the different types of perturbations. The community investigated is generated as detailed in the main text. For each type of perturbation, we applied 100 random perturbations. Error bars correspond to standard error.

the relationship between received interactions and species relative yield, thereby blurring the relationship between species reactivity and their relative yield.

S7. Structuring the interaction network

In our derivation of species reactivity, we assume that all species are connected. However, species in natural ecosystems can be sparsely connected, and the interactions may follow discernible patterns (e.g., nested structures in plant-pollinator networks (Bascompte et al., 2003)). Therefore, we investigate how our results apply to: random interactions (Erdős-Rényi (Erdős, Rényi, et al., 1960)) with a connectance $C \simeq 0.6$, and to a modular structure (Stochastic Block Model (Holland et al., 1983)) of similar connectance. As depicted in figure S5, our results still hold, although the negative trend of the expected reactivity is underestimated. Moreover, we noted that this underestimation increases as the connectance decreases, but the relationships between reactivity against relative yield, and reactivity and response intensity remain. The prediction discrepancy is likely because the connectance of each species should be conditioned by its relative yield. We believe it is feasible to generalize the derivation of the expected reactivity to accommodate specific network structures.

S8. Interplay of species' reactivity and intrinsic resilience

We anticipate that the overall responses of species to perturbations are influenced not only by their reactivity but also by other factors. While species reactivity quantifies short-term responses, it does not fully determine transient and long-term reactions. We propose estimating

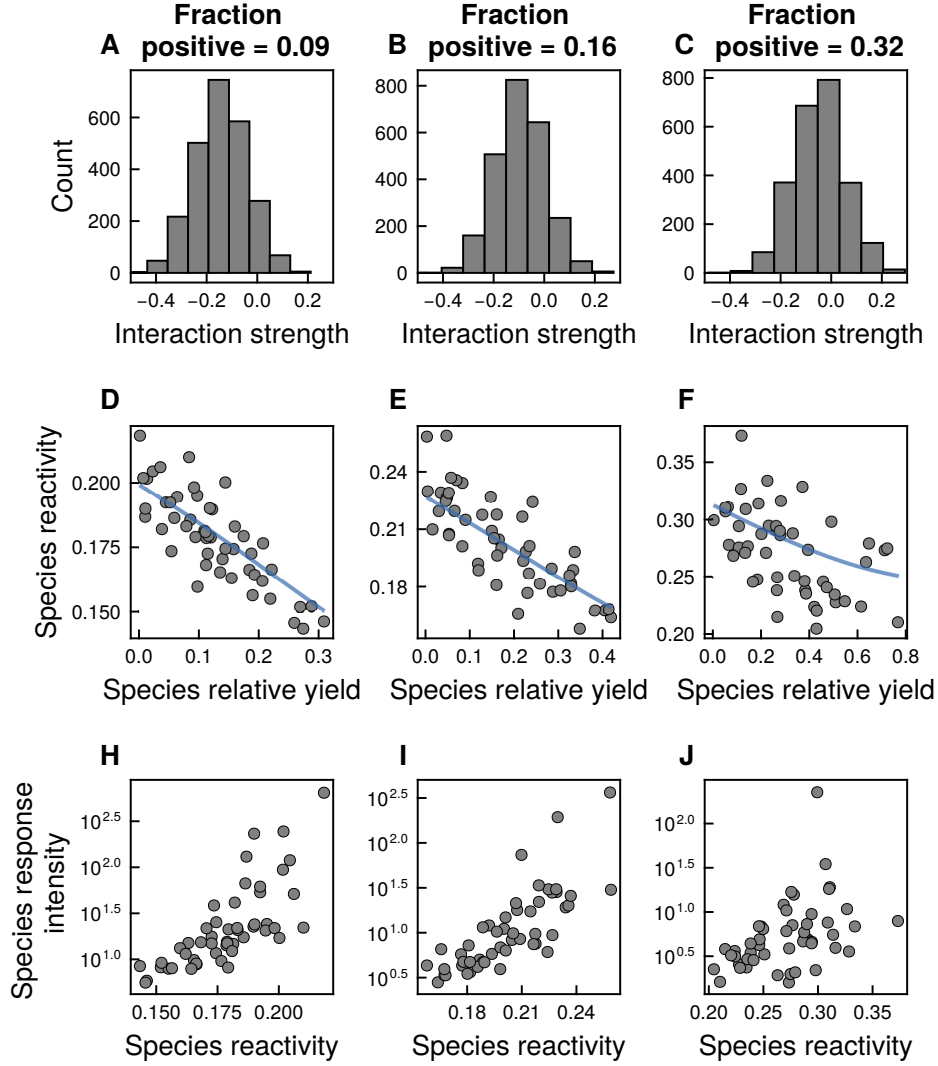


Figure S4 – Impact of adding positive interactions. We examine the relationship between response intensity and reactivity (D-F) and the relationship between species reactivity and relative yield (H-J) for three levels of positive interactions (A-C). To vary the fraction of positive interactions in the community, we randomly draw species interactions (before assembly) from a normal distribution $\mathcal{N}(\mu, 0.1)$, where μ is set to -0.15 , -0.10 , and -0.05 for panels (A, D, H), (B, E, I), and (C, F, J) respectively. Communities are build, and species response intensity is measured as described in the main text. For each fraction of positive interactions, a single community is examined.

the latter using what we term ‘species’ intrinsic resilience’ which equates to its relative yield. Essentially, in the absence of other species, the long-term return rate of a species i is η_i (equation S9), its relative yield. Therefore, in figure S6, we examine the relationship between species’ overall responses and their relative yield, reactivity, and the ratio of the latter to the former, $\frac{R_0^{(i)}}{\eta_i}$. We find that this ratio effectively explains species’ overall response intensity, as expected, given its comprehensive nature encompassing both short- and long-term responses. The relatively modest correlation observed for species’ reactivity can be attributed to its focus on the response to extreme perturbations, which may not represent the typical response to perturbations, whereas we represent the overall response averaged over a vast set of perturbations. Indeed, we demonstrate that the ‘average species reactivity’ representing the expected initial

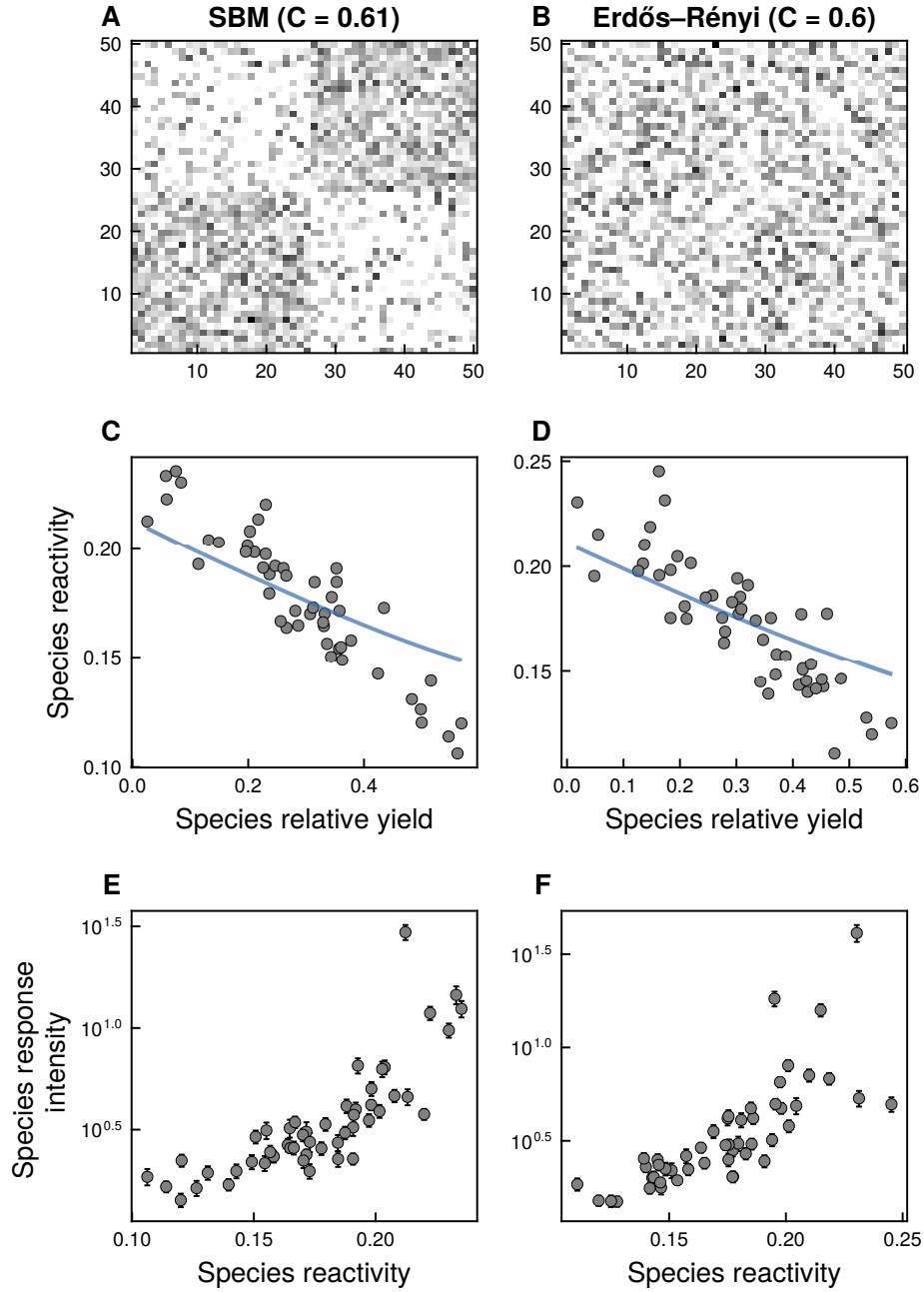


Figure S5 – Impact of structuring the interaction network. We investigate the relationship between response intensity and reactivity (C-D) and the relationship between species reactivity and relative yield (E-F) for two network structures (A-B). In panels (A, C, E), we consider a two-module community generated using the Stochastic Block Model with parameters (mean number of neighbours within a module $n_{\text{intra}} = 24$, and between modules $n_{\text{inter}} = 8$). In panels (B, D, F), we consider an Erdős-Rényi structure with connectance $C = 0.6$. Communities are build, and species response intensity is measured as described in the main text. For each structure, a single community is examined.

response to any perturbation, equals the species' relative yield, signifying its intrinsic resilience (equation S17).

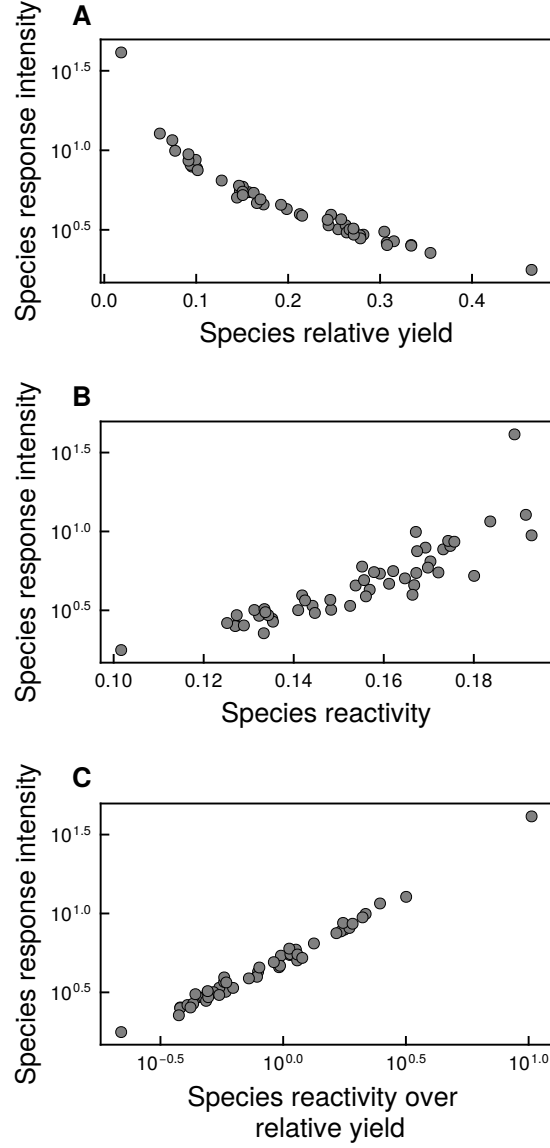


Figure S6 – Species' overall responses to perturbations against species' resilience (A), reactivity (B) and their ratio (C). We assembled a community of $S = 50$ as described in the Material and Methods (Main text) and plotted the overall species' responses against their relative yield (resilience), their reactivity and the ratio of the two latter. Species predictability is averaged over 100 random perturbations. Error bars correspond to standard error.

S9. Derivation of species reactivity

We start from the equation describing the dynamics of our community

$$(S6) \quad \frac{1}{\eta_i} \frac{d\eta_i}{dt} = r_i \left(1 - \eta_i - \sum_{j \neq i} a_{ij} \eta_j \right)$$

From there, we derive the dynamics of species deviation from equilibrium $x_i(t) = \eta_i(t) - \eta_i^*$, with η_i^* given by

$$(S7) \quad \eta_i^* = 1 - \sum_{j \neq i} a_{ij} \eta_j$$

By substituting $\eta_i(t)$ with $x_i(t) - \eta_i^*$ in equation S6, and using equation S7 to simplify terms that cancel out, we obtain

$$(S8) \quad \frac{1}{r_i} \frac{dx_i}{dt} = -\eta_i^* (x_i + \sum_{j \neq i} a_{ij} x_j) - x_i (x_i + \sum_{j \neq i} a_{ij} x_j)$$

In what follows, we focus on the relative deviation to equilibrium, which is $z_i(t) = \frac{x_i(t)}{\eta_i^*}$. We explain in the Material and Methods of the main text and in Section S3 why it is the relevant variable to investigate for our study. Similarly to the derivation of community reactivity, we investigate the linear dynamics of $z_i(t)$

$$(S9) \quad \frac{1}{r_i} \frac{dz_i}{dt} = -\eta_i^* z_i - \sum_{j \neq i} a_{ij} \eta_j^* z_j$$

We see that the RHS of equation S9 can be separated in two terms. The first term only involves the focal species i and characterizes its intrinsic resilience, that is its inclination to return to equilibrium after a disturbance. We remark that the lower the species' relative yield η_i^* , the lower its intrinsic resilience. On the other hand, the second term captures the collective effect of species interactions on the response of the focal species. Importantly, we emphasize that the sum is weighted by the relative yield of the interacting species η_j^* , and that therefore species with low relative yield have little impact on the responses of the other species of the community. Lastly, we find that in the absence of interactions equation S9 becomes trivial, $\frac{dz_i}{dt} = -z_i$, which highlights that our parameterization precisely captures the raw effect of interactions on species responses.

We define the reactivity of species i , as the maximal initial amplification of a perturbation, relatively to its generation time (see Section S2 for more details). Then species reactivity reads

$$(S10) \quad R_0^{(i)} = \max_{\|z(0)\|=1} \left. \frac{1}{r_i} \frac{d|z_i|}{dt} \right|_{t=0}$$

Where the maximum is performed on the set of unitary perturbations $z(0)$. We can set the norm of the perturbation to an arbitrary value because the equation S9 is linear in z_i .

We remark in equation S9 that, to maximize $\frac{d|z_i|}{dt}$, z_i should be null. Indeed, if $z_i > 0$ then $\eta_i^* z_i < 0$ which reduces the value of $\frac{d|z_i|}{dt}$. By contrary, if $z_i < 0$ then $-\eta_i^* z_i > 0$ which also reduces the value of $\frac{d|z_i|}{dt}$. Therefore, we have necessary $z_i = 0$. In this specific case, we can write

$$(S11) \quad \frac{d|z_i|}{dt} = \left| \frac{dz_i}{dt} \right| = r_i \left| \sum_{j \neq i} a_{ij} \eta_j^* z_j \right|$$

Then, applying the Cauchy-Schwarz inequality, we derive

$$(S12) \quad \frac{1}{r_i} \frac{d|z_i|}{dt} \leq \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$$

Additionally, we can verify that the upper bound is attained for the perturbation given by $(z)_j = a_{ij} \eta_j^*$. Hence, we eventually obtain

$$(S13) \quad R_0^{(i)} = \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$$

S10. Average species reactivity

The notion of species reactivity developed above focus on the most extreme perturbation, the perturbation that leads to stronger initial response. However, that response may not be representative of the generic species' response to any perturbation. Therefore, we propose here to derive the 'average species' reactivity, that is, the degree to which a species amplify an initial perturbation on average. To do so, we separate the expected reactivity depending on the sign of the initial perturbation on the focal species. For conciseness, we write

$$\gamma_0 \equiv \left. \frac{d|z_i|}{dt} \right|_{t=0}, \text{ and } \sigma \equiv \mathbb{E}(z_i | z_i > 0)$$

$$(S14) \quad \mathbb{E}(\gamma_0) = \mathbb{E}(\gamma | z_i(0) > 0) p(z_i(0) > 0) + \mathbb{E}(\gamma | z_i(0) < 0) p(z_i(0) < 0)$$

Note that in the expression above, we do not include the expectation for $z_i(0) = 0$, as the corresponding probability is null. For $z_i \neq 0$, we have

$$(S15) \quad \gamma_0 = \text{sign}(z_i(0)) \left. \frac{dz_i}{dt} \right|_{t=0}$$

Therefore, using the linearity of the expectation

$$(S16) \quad \mathbb{E}(\gamma_0) = \frac{1}{2} (-\eta_i^* \sigma + \sum_{j \neq i} a_{ij} \eta_j^* \mathbb{E}(z_j)) - \frac{1}{2} (\eta_i^* \sigma + \sum_{j \neq i} a_{ij} \eta_j^* \mathbb{E}(z_j))$$

In sum

$$(S17) \quad \mathbb{E}(\gamma_0) = -\eta_i^* \sigma \propto -\eta_i^*$$

Then, following a disturbance, on average a species tend to go back directly to its equilibrium at a rate proportional to its relative yield. As a result, the higher the relative yield of the species, the lower its average reactivity. Moreover, we note that species relative yield also correspond to the 'intrinsic resilience' of the species, that is its asymptotic return rate to equilibrium in absence of other species. We therefore see, that species relative yield captures both the short- and long-term behaviour of species responses, which explains the results of the figure S6-A.

S11. Generic prediction for species reactivity

For a given species i , we are looking for an expectation for $|R_0^{(i)}|^2 = \sum_{j \neq i} a_{ij}^2 \eta_j^2$ given that the relative yields η_j are at equilibrium, so satisfy

$$1 - \eta_i = \sum_{j \neq i} a_{ij} \eta_j$$

We further assume a normal prior for interaction terms, which represent how we draw species interactions before the assembly process, supposed to be i.i.d.

$$a_{ij}^{\text{prior}} \sim \mathcal{N}(\mu, \sigma)$$

Let $C = 1 - \eta_i < 1$ let $d = S - 1$ and $u = (\eta_j)_{j \neq i} \in \mathbb{R}_+^d$. Let $X_j^{\text{prior}} = a_{ij}^{\text{prior}}$ written as $X_j^{\text{prior}} = \mu + Z_j^{\text{prior}}$ where the Z_j^{prior} are d i.i.d normal random variables with zero mean and variance σ^2 . Let X_j^{post} be the random variables conditioned by observations of equilibrium values (Bunin, 2017). If we denote the standard scalar product $\langle w | v \rangle = \sum_{j=1}^d w_j v_j$, for any vectors w, v in \mathbb{R}^d we can write the equilibrium condition as

$$C = \langle X^{\text{post}} | u \rangle = \mu \langle 1 | u \rangle + \langle Z^{\text{post}} | u \rangle$$

In what follows we will make use of 'bra-ket' notation for dual vectors and vectors respectively, mapped to one-another by the standard scalar product $\langle \cdot | \cdot \rangle$. A vector is a 'ket' noted $|v\rangle$ while a dual vector is a 'bra' noted $\langle w|$. A 'bra' acts on a 'ket' as $\langle w| : |v\rangle \mapsto \langle w | v \rangle$ to give the scalar product, the 'bra-ket', of the two vectors. Conversely a 'ket-bra' of the form $|v\rangle \langle w|$ is a linear application from \mathbb{R}^d to \mathbb{R}^d (so a square matrix), $|v\rangle \langle w| : |x\rangle \mapsto |v\rangle \langle w | x \rangle$. We will also use some norms, for any vector $v \in \mathbb{R}^d$,

$$\|v\|_q = \left(\sum_{j=1}^d |v_j|^q \right)^{1/q}$$

in practice only $q = 1, 2, 3, 4$ will come up. We then define normalized quantities and vectors

$$\tilde{C} = \frac{C}{\|u\|_2}; \quad |\tilde{u}\rangle = \frac{|u\rangle}{\|u\|_2}$$

The key idea is to build an orthonormal basis of \mathbb{R}^d starting from $|\tilde{u}\rangle$, and defining $d - 1$ orthonormal vectors $|v_\lambda\rangle$. Then, because the distribution of Z^{prior} is isotropic, the conditioning do not affect its components in the subspace spanned by $|v_\lambda\rangle$, and we may write

$$|Z^{\text{post}}\rangle = \sum_{\lambda=1}^{d-1} Y_\lambda |v_\lambda\rangle + \left(\tilde{C} - \mu \langle \tilde{u} | 1 \rangle \right) |\tilde{u}\rangle$$

where the non-conditioned part of Z^{post} is encoded in $d - 1$ i.i.d random variables $Y_\lambda \sim \mathcal{N}(0, \sigma)$. If Z^{prior} had not being isotropic, we would have had to properly rotate its covariance matrix, and project it on the unconditioned hyperplane. Decomposing the vector $\mu |1\rangle$ on the above basis leads to

$$|X^{\text{post}}\rangle = \sum_{\lambda=1}^{d-1} Y_\lambda |v_\lambda\rangle + \mu P_u^\perp |1\rangle + \tilde{C} |\tilde{u}\rangle$$

where $P_u^\perp = \mathbb{I} - |\tilde{u}\rangle \langle \tilde{u}|$ is the projector on the orthogonal plane to u . We can check that the equilibrium condition is automatically satisfied for X^{post} . From here we can get the conditional expectation

$$\mathbb{E} X_j^{\text{post}} = \mu (1 - \langle \tilde{u} | 1 \rangle \tilde{u}_j) + \tilde{C} \tilde{u}_j$$

which in the original variables become

$$\mathbb{E}a_{ij} = \mathbb{E}a_{ij}^{\text{prior}} \left(1 - \frac{\|\eta\|_1 - \eta_i}{\|\eta\|_2^2 - \eta_i^2} \eta_j \right) + \frac{1 - \eta_i}{\|\eta\|_2^2 - \eta_i^2} \eta_j$$

What we need however, are the second moments of X^{post} . To get to those we may start from

$$|X^{\text{post}}\rangle \langle X^{\text{post}}| = \left(\sum_{\lambda} Y_{\lambda} |v_{\lambda}\rangle + |P_u^{\perp} \mu\rangle + \tilde{C} |\tilde{u}\rangle \right) \left(\sum_{\gamma} Y_{\gamma} \langle v_{\gamma}| + \langle P_u^{\perp} \mu| + \tilde{C} \langle \tilde{u}| \right)$$

Whose expected value is

$$\mathbb{E} |X^{\text{post}}\rangle \langle X^{\text{post}}| = \sigma^2 P_u^{\perp} + |P_u^{\perp} \mu\rangle \langle P_u^{\perp} \mu| + \tilde{C} (|P_u^{\perp} \mu\rangle \langle \tilde{u}| + |\tilde{u}\rangle \langle P_u^{\perp} \mu|) + \tilde{C}^2 P_u$$

So that

$$\mathbb{E}(X_j^{\text{post}})^2 = \sigma^2(1 - \tilde{u}_j^2) + \mu^2 (1 - 2\|\tilde{u}\|_1 \tilde{u}_j + \|\tilde{u}\|_1^2 \tilde{u}_j^2) + 2\mu \tilde{C}(\tilde{u}_j - \|\tilde{u}\|_1 \tilde{u}_j^2) + \tilde{C}^2 \tilde{u}_j^2$$

We now want to compute

$$\sum_{j=1}^d \mathbb{E}(X_j^{\text{post}})^2 \tilde{u}_j^2 = \overline{\mathbb{E}a_{ij}^2}$$

which is a weighted average (recall that $\sum \tilde{u}_j^2 = 1$ by definition), of conditional expectations.

Eventually, we obtain

$$(S18) \quad \mathbb{E}|R_0^{(i)}|^2 = \overline{\mathbb{E}a_{ij}^2} \times \|u\|_2^2 = \overline{\mathbb{E}a_{ij}^2} \times (\|\eta\|_2^2 - \eta_i^2)$$

Where we have

$$(S19) \quad \begin{aligned} \overline{\mathbb{E}a_{ij}^2} &= \mathbb{E}(a_{ij}^{\text{prior}})^2 \left(1 - \frac{1}{D_{/i}^{(4)}}\right) + \dots \\ &\dots + \frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} \left(\frac{1 - \eta_i}{\|\eta\|_1 - \eta_i}\right)^2 + \dots \\ &\dots - 2(\mathbb{E}a_{ij}^{\text{prior}}) \left(\frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} - \sqrt{\frac{D_{/i}^{(2)}}{D_{/i}^{(3)}}}\right) \frac{1 - \eta_i}{\|\eta\|_1 - \eta_i} + \dots \\ &\dots - (\mathbb{E}a_{ij}^{\text{prior}})^2 \left(2\sqrt{\frac{D_{/i}^{(2)}}{D_{/i}^{(3)}}} - \frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} - \frac{1}{D_{/i}^{(4)}}\right) \end{aligned}$$

And we introduced three, non-equivalent, diversity measures for the community of all species but the focal species i .

$$d \geq \|\tilde{u}\|_1^2 =: D_{/i}^{(2)} \geq (\|\tilde{u}\|_3^3)^{-2} =: D_{/i}^{(3)} \geq (\|\tilde{u}\|_4^4)^{-1} =: D_{/i}^{(4)} \geq 1$$

In figure S7-A, we compare the full prediction derived above, which takes into account the dependency of the expected interactions given the species relative yield, with the naive prediction obtained by substituting $\mathbb{E}(a_{ij}^2)$ with $\mathbb{E}(a_{ij}^{\text{prior},2})$. We observe that the naive prediction fails to predict the trend accurately, while the full prediction does so effectively. The discrepancy between the naive prediction and the true species reactivity stems from the fact that species with low relative yield also receive stronger interactions, amplifying the decreasing trend (figure S7-B). Thus, this highlights the importance of considering the dependency between interactions and species relative yield to accurately predict reactivity.

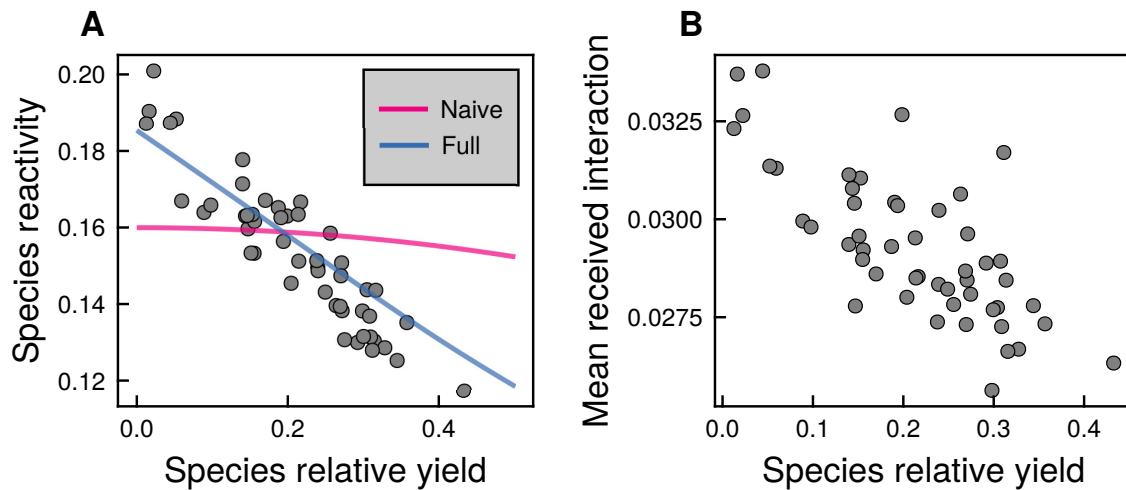


Figure S7 – Predictions of species reactivity. A) Naive vs. full prediction for species reactivity. The full prediction accounts for the dependency between mean interactions received by species $\mathbb{E}a_{ij}^2$ and species relative yield, while the naive does not. B) Relationship between the mean received interaction received by species and their relative yield. We observe a clear decreasing trend, which explains why the naive prediction – which ignore this dependency – underestimates the decreasing of species reactivity with relative yield.

References

- Barbier M, De Mazancourt C, Loreau M, Bunin G (2021). *Fingerprints of high-dimensional coexistence in complex ecosystems*. *Physical Review X* **11**, 011009.
- Bascompte J, Jordano P, Melián CJ, Olesen JM (2003). *The nested assembly of plant–animal mutualistic networks*. *Proceedings of the National Academy of Sciences* **100**, 9383–9387.
- Bunin G (2017). *Ecological communities with Lotka-Volterra dynamics*. *Physical Review E* **95**, 042414.
- Carrara F, Giometto A, Seymour M, Rinaldo A, Altermatt F (2015). *Inferring species interactions in ecological communities: a comparison of methods at different levels of complexity*. *Methods in Ecology and Evolution* **6**, 895–906.
- Erdős P, Rényi A, et al. (1960). *On the evolution of random graphs*. *Publ. math. inst. hung. acad. sci* **5**, 17–60.
- Holland PW, Laskey KB, Leinhardt S (1983). *Stochastic blockmodels: First steps*. *Social networks* **5**, 109–137.
- Loreau M (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46)*. Princeton University Press.
- Loreau M, Hector A (2001). *Partitioning selection and complementarity in biodiversity experiments*. *Nature* **412**, 72–76.
- Neubert MG, Caswell H (1997). *Alternatives to resilience for measuring the responses of ecological systems to perturbations*. *Ecology* **78**, 653–665.
- Trefethen LN (2005). *Spectra and Pseudospectra: The Behaviour of Non-normal Matrices and Operators*. In: *The graduate student's guide to numerical analysis' 98: Lecture notes from the VIII EPSRC Summer School in Numerical Analysis*. Springer, pp. 217–250.