

How biotic interactions structure species' responses to perturbations

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Abstract

Predicting how ecological communities will respond to disturbances is a major challenge in community ecology, 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 complexity of the network of biotic interactions, species' responses follow a discernible pattern. Specifically, we demonstrate that species whose abundance 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.

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 has many meanings (Ives and Carpenter, 2007; Donohue et al., 2013, 2016; Kéfi et al., 2019), reflecting the rich history of the field. Intuitively, stability ought to characterize the way a community responds to environmental disturbances. In fact, one classic approach is to equate stability with the capacity of a community to revert to its original state after a disturbance, assuming the latter did not push the system 'too far' (May, 1973). In this particular sense, stability focuses on the eventual recovery of communities (Arnoldi et al., 2018).

That being said, there is a growing recognition that the response of communities to disturbances is multi-dimensional, a realization that cautions against trying to capture it by a single measure of ecological stability (Donohue et al., 2013, 2016; Pennekamp et al., 2018; Arnoldi et al., 2019; Kéfi et al., 2019). This multidimensional nature of ecological responses to disturbances is in part due to the fact that any response evolves over time. Even if a community eventually recovers (*i.e.* is stable in the above conventional sense), it may still exhibit a great 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 and 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 ability to initially amplify a perturbation (Neubert and Caswell, 1997). In ecology, (Tang and 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.

Reactivity, however, has been conceptualized at the system level 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, while in reality some of its constituent species will undergo large variations of their population size, and be at risk of local extinction (Supp and Ernest, 2014). More generally, to derive tangible ecological predictions of community recovery, it is crucial to understand how response 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. Our approach involves quantifying response intensity, where high intensity indicates nonlinear population dynamics following a pulse perturbation, and a risk of extinction. In theory, recovery dynamics can be predicted 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 remain 'close' to their unperturbed state

immediately after a disturbance and throughout their recovery. However, even after a mild perturbation, species 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 such species becomes unpredictable. Such phenomena may in turn undermine the predictability of the recovery of the whole community (Neubert and Caswell, 1997).

Our theoretical framework seeks to characterize how species response intensity is structured 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. We thus 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 in 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 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 and 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 (Fig. 1-A). The lower a species' relative yield is, the more its equilibrium abundance has been reduced by the effect of biotic interactions.

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 (Fig. 1-A). As we want to separate the variability of species responses due to differences in species demographic traits from differences due to interactions, we consider a non-dimensional timescale t_i for each species (*e.g.* time measured in units of the species generation time). We model the dynamics of the species relative yields as a Lotka-Volterra system, which is entirely parameterized by non-dimensional interaction terms, denoted a_{ij} (Fig. 1-B):

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

The community steady state is given by $\boldsymbol{\eta}^*$, the vector of species relative yields at equilibrium, which cancels the derivative of Eq. 1 for all species.

Deviation from equilibrium We write $x_i = \eta_i - \eta_i^*$ the deviation of species i to its equilibrium. The temporal evolution of this deviation reads:

$$\frac{dx_i}{dt_i} = -\underbrace{\eta_i^* (x_i + \sum_{j \neq i} a_{ij} x_j)}_{\text{linear}} - \underbrace{x_i (x_i + \sum_{j \neq i} a_{ij} x_j)}_{\text{nonlinear}} \quad (2)$$

We see here that non-linear dynamics can only be neglected if $|x_i(t)| < \eta_i^*$, for all i , and all times t . Thus, if the variable $z_i(t) = x_i(t)/\eta_i^*$ is much smaller, in absolute value, than 1. We can thus see $|z_i(t)|$ as a measure of the non-linearity of species i 's dynamics at time t . We will use this measure of nonlinearity to quantify how strongly species respond to perturbations. In sum, this change in variables allow pinpointing the limits of the linear approximation, which consist in neglecting the nonlinear term of Eq. 2. In addition, from a conservation perspective, z_i is the normalized variable which captures the risk of species extinction. Indeed

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

and we see that species i becomes extinct if $z_i = -1$ at some time t .

Quantifying species' response intensity Even if the initial perturbation on a species is weak (in the above sense), it may still elicit a strong response during the transient dynamics. We propose to capture this phenomenon by defining a notion of 'species reactivity', which quantifies how strongly an initial perturbation can be amplified by each species population dynamics.

To derive an analytical expression for the species reactivity we start from the linear dynamics of z_i :

$$\frac{dz_i}{dt_i} = -\eta_i^* z_i - \sum_{j \neq i} a_{ij} \eta_j^* z_j \quad (4)$$

We see that the right-hand side of Eq. 4 can be separated in two terms. The first term only involves the focal species i and characterizes its intrinsic resilience, *i.e.* 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 and, in addition, this term controls the species reactivity. 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 Eq. 4 becomes trivial, $\frac{dz_i}{dt_i} = -z_i$, which highlights that our parameterization precisely captures the raw effect of interactions on species responses. Then, we can show that the initial derivative of the nonlinearity of species i verifies (see Supporting Information for proof):

$$\frac{1}{\|z(0)\|} \left. \frac{d|z_i|}{dt_i} \right|_{t=0} \leq \sqrt{\sum_{j \neq i} (a_{ij} \eta_j^*)^2} \equiv R_0^{(i)} \quad (5)$$

The upper bound of the inequality corresponds to the stronger increase of an initial perturbation, that is what we define as the species reactivity $R_0^{(i)}$. $R_0^{(i)}$ is always positive, which means that for any species, there always exists a perturbation which leads to an initial increase of its nonlinearity.

Species reactivity characterizes, therefore, the short-term behaviour of species' responses, yet we expect that it is a good indicator of the overall species response intensity, a claim that will test on simulated communities (see Fig. 1-C, and 'Simulations' section).

Expectation To demonstrate why and how the variability in species responses is structured by the distribution of species relative yields, we derive an analytical expectation for species reactivity. Here we present the main-lines of the derivation and their ecological implications, for the full derivation please refer to the Supporting Information.

Following (Bunin, 2017), this expectation aims at using knowledge of species relative yields, plus minimal information about the pairwise interactions to predict the overall intensity of interactions felt by each species, to then deduce their reactivity. We start from a normal prior for the set of interaction strengths (a_{ij}) , to deduce conditional expectations for interaction terms a_{ij}^2 , noted $\mathbb{E}[a_{ij}^2 | \boldsymbol{\eta}^*]$. From there, we deduce a conditional

expectation for $(R_0^{(i)})^2 = \sum_{j \neq i} a_{ij}^2 \eta_j^{*2}$, which reads:

$$\mathbb{E}[(R_0^{(i)})^2 | \boldsymbol{\eta}^*] = \overline{\mathbb{E}[a_{ij}^2 | \boldsymbol{\eta}^*]} \times (\|\boldsymbol{\eta}^*\|^2 - \eta_i^{*2}) \quad (6)$$

In this expression, $\overline{\mathbb{E}[a_{ij}^2 | \boldsymbol{\eta}^*]}$ is a weighted average of expected absolute interactions a_{ij}^2 (weights are determined by the relative yields of species that interact with the focal species i), and $\|\boldsymbol{\eta}^*\|$ is the Euclidean norm of the vector of relative yields. From here we distinguish two approximations. The simplest assumes that the expected interactions are independent of species relative yields, so that we may replace $\overline{\mathbb{E}[a_{ij}^2 | \boldsymbol{\eta}^*]}$ with the unconditioned prior $\mathbb{E}[a_{ij}^2]$. This leads us to our ‘naive’ expectation of species reactivity. As we shall see however, this approximation is too crude. We get a more sophisticated prediction by deriving an analytical expression for $\overline{\mathbb{E}[a_{ij}^2 | \boldsymbol{\eta}^*]}$ which accounts for the fact that interactions and relative yields are not independent from one another. This leads us to our ‘full’ expectation of species reactivity.

Simulations

Community assembly We assemble species-rich communities made of $S = 50$ species, with interactions a_{ij} drawn from a truncated normal distribution $a_{ij} \sim |\mathcal{N}(0, \sigma^2)|$, thus modelling purely competitive communities with mean interaction strength $\sqrt{\frac{2}{\pi}}\sigma$ ($\sigma = 0.1$). For the sake of simplicity, we considered that all species had the same timescale t_i .

Community perturbations We consider that species are, on average, disturbed proportionally to their unperturbed abundance (Arnoldi et al., 2018). In terms of relative yields, this simply amounts to perturbing the latter proportionally to their unperturbed values. To generate such a perturbation, we generate a vector whose coefficients are drawn independently in $x_i \sim \mathcal{N}(0, 1)$ and then multiply these coefficients by the corresponding unperturbed relative yield. The amplitude of the perturbations is set such that: $\sqrt{\langle z_i(0)^2 \rangle_i} = 0.6$.

Overall response intensity Species reactivity quantifies, by definition, a species short-term species response to a pulse perturbation. However, 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 (Fig. 1-C). To test this idea, we first define overall response intensity $I(T)$ as:

$$I(T) = \frac{1}{T} \frac{1}{|y(0)|} \int_0^T |y(t)| dt \quad (7)$$

Where y is the distance of interest to the equilibrium, and T the duration of observation (numerically, $T = 1,000$). For species, we take $y = z$ the nonlinearity of the species. For communities, we take $y = \Delta N_{\text{tot}}$ the deviation of the community total abundance to its equilibrium value.

Selection effect Consistently with the seminal work of (Loreau and Hector, 2001), we define the ‘selection effect’ as the covariance between the relative yield of species and their carrying capacity. To investigate the impact of the sign of the selection effect on the relationship between the species reactivity and their equilibrium abundance, we consider the three following carrying capacity distributions:

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

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

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

where ε_i is a random term drawn in $\mathcal{N}(0, 1)$. 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 and 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 the reactivity of species, which quantifies the ability of a species to amplify an initial perturbation:

$$R_0^{(i)} = \sqrt{\sum_{j \neq i} (a_{ij} \eta_j^*)^2} \quad (11)$$

For context, a reactivity value of 1 means that after 1 unit of the species' characteristic time, the species would experience a 100% change in its abundance. Surprisingly, the reactivity of a species depends only on the interactions directed towards it. 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 Fig 2-A. As predicted by both of our analytical expectations, 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 reveal that while the 'full' expectation effectively accounts for the diminishing slope of species reactivity with relative yield, the 'naive' expectation underestimates this decrease. This indicates that the decline in species reactivity with their relative yield is shaped by two factors. Firstly, an increase in species' relative yield inherently leads to a reduction in species reactivity. However, solely considering this aspect, as captured by the 'naive' expectation, does not fully explain the observed variation. Secondly, an increase in species' relative yield is also associated with weaker received interactions (a_{ij}^2), which consequently leads to a decrease in reactivity (Eq. 11). This latter factor elucidates the disparities observed in the 'naive' expectation.

Moreover, we anticipate that the species reactivity, while assessing the species' short-term response to perturbations, provides information on the overall response of the species, encompassing the entire recovery. To validate that expectation, we measure the intensity of the species' overall response to perturbations (Fig. 1-C) and plot it against the species reactivity (Fig. 2-B). As anticipated, we observe that species reactivity serves as a reliable proxy to assess the species' overall response intensity to perturbations. Therefore, we can confidently use the reactivity of species to quantify how strongly species respond to disturbance. Furthermore, we note that species relative yield is also a strong predictor of species overall response intensity (Fig. S2). Finally, we confirm that stronger species responses are harder to predict with the linear approximation (Fig. S1).

In sum, these results indicate that the relative yield determines the intensity of species responses to perturbations. However, the relative yield is often unavailable in data, as species carrying capacities are typically unobserved. Conversely, species abundances are usually known in the data. Therefore, we aim to establish a relationship between species reactivity and abundance in the following analysis.

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

We can now unravel the missing link between the reactivity of species and their abundance using the ‘selection effect’ concept of (Loreau and 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). For instance, 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. Indeed, species relative yield and abundance are not necessarily positively correlated, a rare species in the community can be abundant alone and conversely.

As a result, we illustrate in Fig. 3 that for a given species reactivity-relative yield relationship (Fig. 3-A), we can observe different species reactivity-abundance relationships depending on the sign of the selection effect (Fig. 3-B-D). More specifically, we show that a positive selection effect leads to a decrease in species reactivity with their abundance (Fig. 3-B), while a negative selection effect leads to a null or positive trend between reactivity and abundance (Fig. 3-C, D). We anticipate that the sign of the reactivity-abundance relationship impacts the response of the whole community.

Therefore, we show that the relationship between the reactivity of species and their abundance – reflecting the selection effect – determines the intensity of the response of the entire community, defined in the terms of total community abundance. We illustrate the distribution of the community response intensities for the three abundance-reactivity relationships previously investigated: negative, null or positive (Fig. 3-D). We see that the community with a negative selection effect exhibit stronger responses to perturbations than the community with a positive selection effect.

We have explored above different possible scenarios by discussing the sign of the selection effect and unravelling its impact on how strongly the entire community responds to perturbations. Next, we investigate these relationships in empirical data from a plant community using the conceptual framework developed here.

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 (refer to Material and Methods). We first plot the reactivity of species against their relative yield (Fig 4-A). Notably, we observe a consistent decrease in species reactivity with their relative yield, mirroring the pattern observed in randomly parameterized communities (Fig 2-A). Moreover, we find that our theoretical expectation of species reactivity closely aligns with the observed data (solid lines in Fig 4-A), despite being based on assumptions that may not hold true in natural communities, such as normally distributed interactions.

Next, we examine the relationship between species reactivity and their abundance in communities displaying a positive selection effect (Fig 4-B) and a negative one (Fig 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 Fig 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.

Therefore, we investigate how the selection effect influences the response intensity of the entire community. To achieve this, we illustrate the distribution of community response intensities separately for communities exhibiting positive and negative selection effects (Fig 4-C). Our results aligns with the findings in Fig. 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. A common strategy is to model these communities as complex dynamical systems and view perturbations as deviations from 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 and Ernest, 2014). Our approach breaks down community responses to the species level, shedding light on how the intensity of species' responses is organized. This, in turn, allows to make novel predictions regarding whole community responses.

We find 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 data processed from grassland experiments, only depends on basic summary statistics of the set of biotic interactions. In essence, we develop a method for identifying sensitive species in ecological communities without needing detailed information about species interactions.

Unpredictability of sensitive species

In theoretical work, 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.

However, 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 species can exhibit reactive behaviour during their transient recovery, venturing 'far' from their equilibrium. Rather than viewing this observation as a theoretical limitation, we leverage it to *define* a

concept of response intensity and *species reactivity*.

To achieve this, we quantify a species' response intensity in a manner that directly relates to the nonlinearity of its population dynamics. Therefore, by demonstrating that species experiencing the greatest reductions in abundance due to biotic interactions exhibit heightened responses to perturbations, we also establish that such species are likely to manifest transient responses that are hard to predict.

Beyond individual species: unveiling community responses to disturbances

Species exhibiting the strongest responses to disturbances may vary in their abundance between communities. Some communities feature these species as the most abundant, while in others, they are the least abundant. Our study reveals that this relationship between species' sensitivities to perturbations and their relative abundance is driven by the sign of the 'selection effect' characterizing a community's assembly pattern (Loreau and Hector, 2001). Specifically, when the selection effect within the community is negative, the most responsive species also tend to be the most abundant. Consequently, given that abundant species inherently contribute significantly to the total community abundance, such communities are prone to displaying strong responses to perturbations.

This result raises two key questions: 1) how can we evaluate the selection effect using limited data? and 2) how common are communities with negative selection effect 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. Secondly, the seminal study of (Loreau and 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 and Caswell, 1997) commonly used in ecology (Tang and 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 is anticipated as 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

collective behaviour reliant on specific arrangement of species dynamics, while species reactivity pertains solely to individual population behaviours.

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 remain 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 to understand 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 and Gilliam, 2001; Galiana et al., 2021).

Although it may appear that we have reached a dead end, this may suggest to turn 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 framework suggests that species' responses to disturbances could provide insights into inferring the interaction network of the community, which is notoriously challenging (Carrara et al., 2015).

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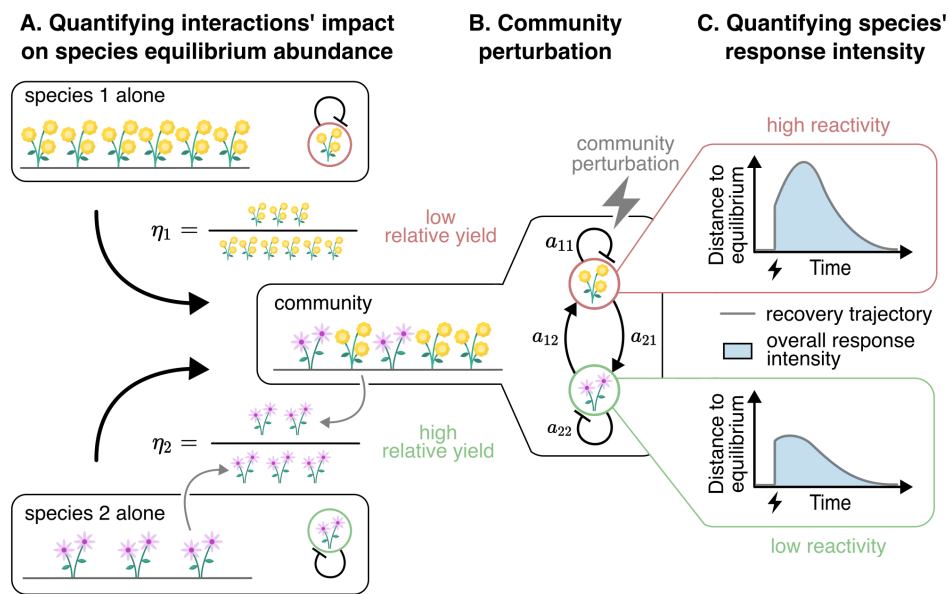


Figure 1. Visual summary. A) When assembled in a community, species equilibrium abundances can rise or fall because of interactions. We quantify this impact of interactions on species equilibrium abundance with the relative yield of species $\eta_i = \frac{N_i}{K_i}$, with N_i is the species abundance 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.

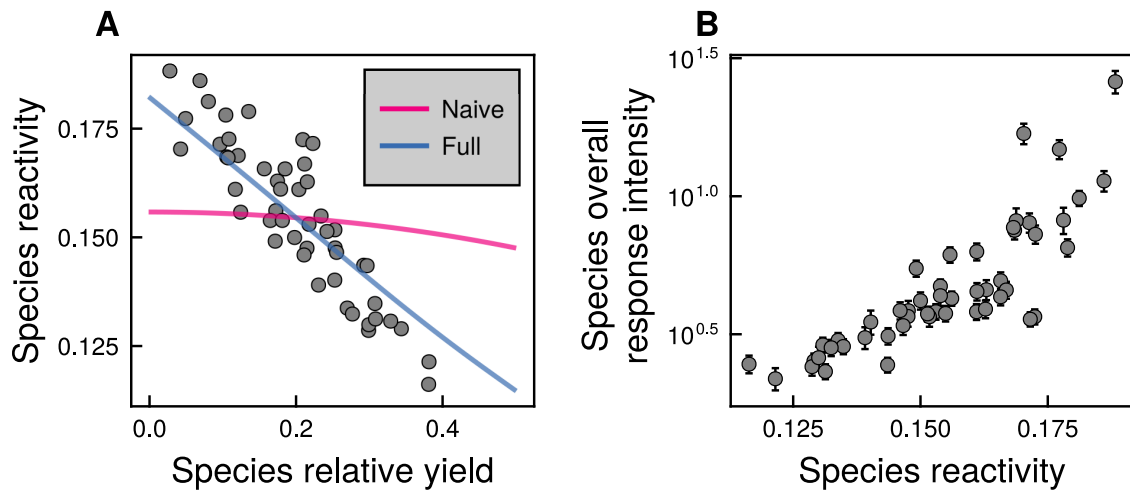


Figure 2. Species whose abundance is most reduced by biotic interactions exhibit stronger responses to perturbations. A) The reactivity of species (their worst-case initial response to pulse-perturbations) against their relative yield, which quantifies the impact of biotic interactions on species' equilibrium abundance. The solid lines correspond to theoretical expectations of species reactivity derived in the Material and Methods. 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.

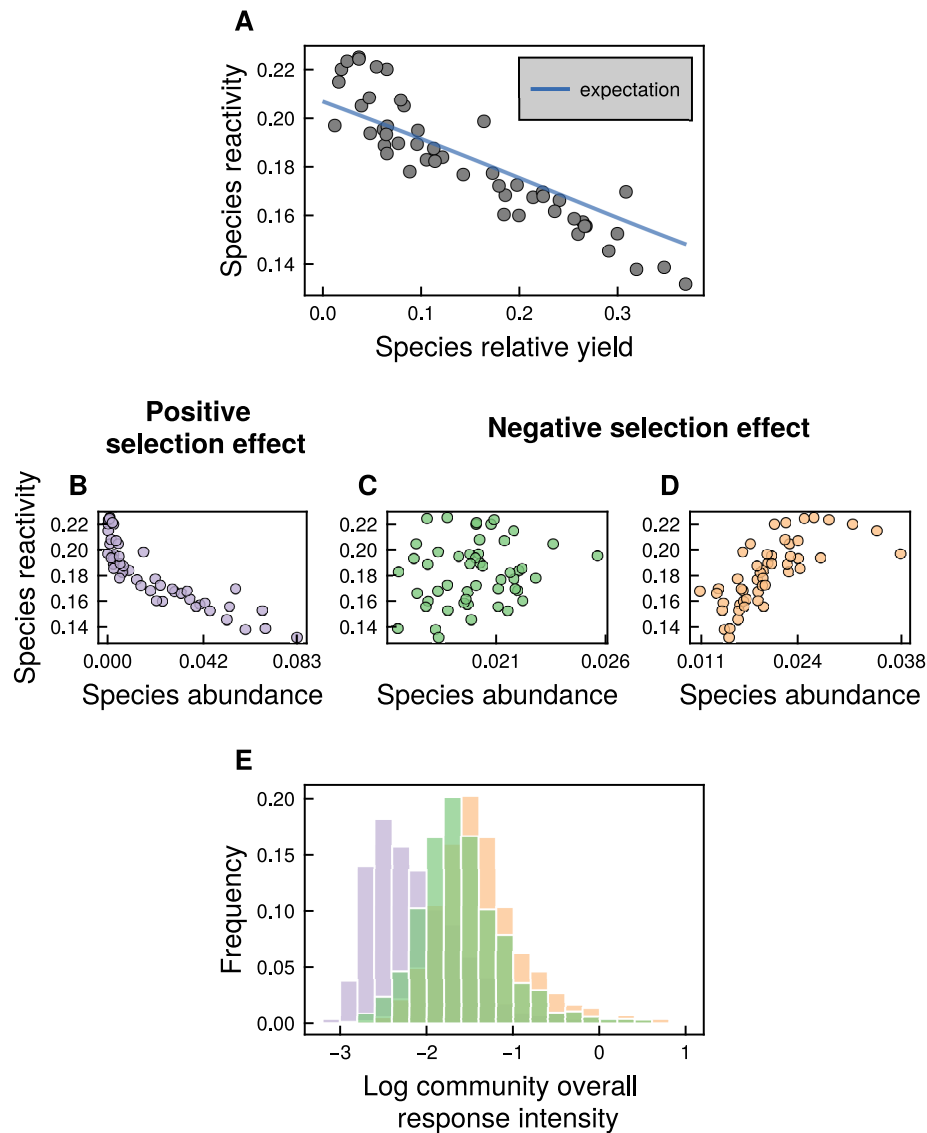


Figure 3. Selection effect indicates how strongly communities respond to perturbations. A) The reactivity of species against their relative yield for a single community. The blue solid line corresponds to the theoretical full expectation (see Material and Methods). B-D) The same species reactivity-relative 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).

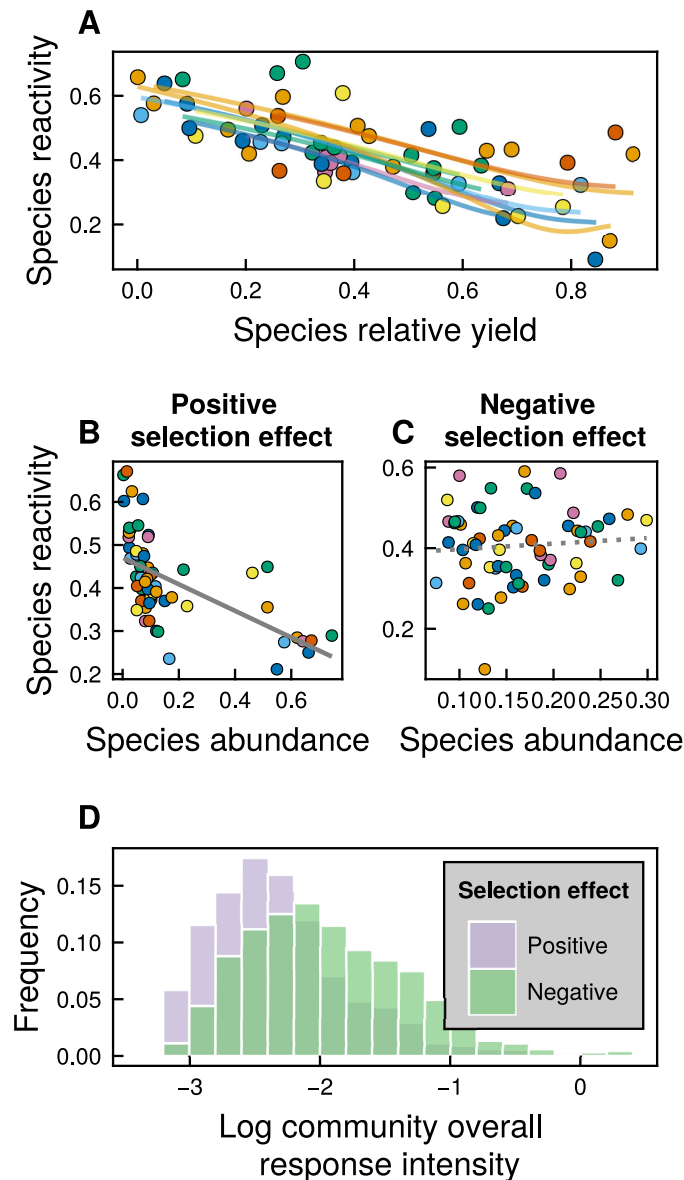


Figure 4. The structure of the variability in species response intensity inform on the responses of communities parameterized from grassland community data. A) The reactivity of species against their relative yield for 10 communities parameterized using empirical data. Each colour corresponds to one 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.

SUPPORTING INFORMATION TO

How biotic interactions structure species' responses to perturbations

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1 Derivation of species reactivity

We define the reactivity of species i , as the maximal value of the derivative of species' relative distance to its equilibrium $|z_i| = \frac{|\eta_i - \eta_i^*|}{\eta_i^*}$.

$$\max_{\mathbf{z}(0) \in \mathbb{R}^S} \frac{1}{\|\mathbf{z}(0)\|} \left. \frac{d|z_i|}{dt} \right|_{t=0} \quad (\text{S1})$$

To do so, we start from Eq. 4 describing the linear dynamics of z_i :

$$\frac{dz_i}{dt} = -\eta_i^* z_i + \sum_{j \neq i} a_{ij} \eta_j^* z_j \quad (\text{S2})$$

First, we remark 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

$$\frac{d|z_i|}{dt} = \left| \frac{dz_i}{dt} \right| = \left| \sum_{j \neq i} a_{ij} \eta_j^* z_j \right| \quad (\text{S3})$$

Then, applying the Cauchy-Schwarz inequality, we derive

$$\frac{1}{\|\mathbf{z}(0)\|} \left. \frac{d|z_i|}{dt} \right| \leq \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}} \quad (\text{S4})$$

Additionally, we can verify that the upper bound is attained for $z_j = a_{ij} \eta_j^*$. Hence, we define species reactivity as $R_0^{(i)} = \sqrt{\sum_j a_{ij}^2 \eta_j^{*2}}$.

2 Expectation 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, supposed to be i.i.d.

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

Let $C = 1 - \eta_i < 1$ let $d = S - 1$ and $u = (\eta_j)_{j \neq i} \in \mathbb{R}_+^d$. Let $X_j^{prior} = a_{ij}^{prior}$ written as $X_j^{prior} = \mu + Z_j^{prior}$ 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. 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

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

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

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

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

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

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

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

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

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

which in the original variables become

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

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

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

Whose expected value is

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

So that

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

We now want to compute

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

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

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

To clarify the resulting calculation, we introduce three, non equivalent, diversity measures for the community of all species but the focal species i .

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

to show that

$$\begin{aligned}
\overline{\mathbb{E}a_{ij}^2} &= \mathbb{E}(a_{ij}^{prior})^2 \left(1 - \frac{1}{D_{/i}^{(4)}}\right) + \dots \\
\dots + &\frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} \left(\frac{1-\eta_i}{\|\eta\|_1 - \eta_i}\right)^2 + \dots \\
\dots - &2(\mathbb{E}a_{ij}^{prior}) \left(\frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} - \sqrt{\frac{D_{/i}^{(2)}}{D_{/i}^{(3)}}}\right) \frac{1-\eta_i}{\|\eta\|_1 - \eta_i} + \dots \\
\dots - &(\mathbb{E}a_{ij}^{prior})^2 \left(2\sqrt{\frac{D_{/i}^{(2)}}{D_{/i}^{(3)}}} - \frac{D_{/i}^{(2)}}{D_{/i}^{(4)}} - \frac{1}{D_{/i}^{(4)}}\right)
\end{aligned} \tag{S5}$$

3 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 derivate 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

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

$$\mathbb{E}(\gamma_0) = \mathbb{E}(\gamma | z_i(0) > 0) p(z_i(0) > 0) + \mathbb{E}(\gamma | z_i(0) < 0) p(z_i(0) < 0) \tag{S6}$$

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

$$\gamma_0 = \text{sign}(z_i(0)) \frac{dz_i}{dt} \Big|_{t=0} \tag{S7}$$

Therefore, using the linearity of the expectation

$$\mathbb{E}(\gamma_0) = \frac{1}{2} \left(-\eta_i^* \sigma + \sum_{j \neq i} a_{ij} \eta_j^* \mathbb{E}(z_j) \right) - \frac{1}{2} \left(\eta_i^* \sigma + \sum_{j \neq i} a_{ij} \eta_j^* \mathbb{E}(z_j) \right) \tag{S8}$$

In sum

$$\mathbb{E}(\gamma_0) = -\eta_i^* \sigma \propto -\eta_i^* \tag{S9}$$

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.

4 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

$$\Delta_i = \frac{\int_{\mathbb{R}^+} |z_i(t) - \hat{z}_i(t)| dt}{\int_{\mathbb{R}^+} |z_i(t)| dt} \tag{S10}$$

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

$$\rho_i = e^{-\Delta_i} \tag{S11}$$

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 Fig. 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.

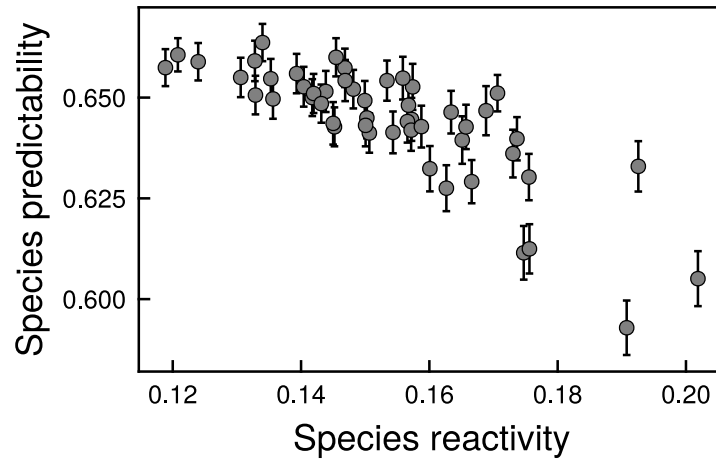


Figure S1. Species' responses to perturbations becomes increasingly harder-to-predict, as species becomes more reactive. We assembled a community of $S = 50$ as described in the Material and Methods (Main text) and plotted the reactivity of species against their predictability. Species predictability is averaged over 1,000 random perturbations. Error bars correspond to standard error.

5 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 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 (Eq. S2), its relative yield. Therefore, in Figure S2, 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 response to any perturbation, equals the species' relative yield, signifying its intrinsic resilience (Eq. S9).

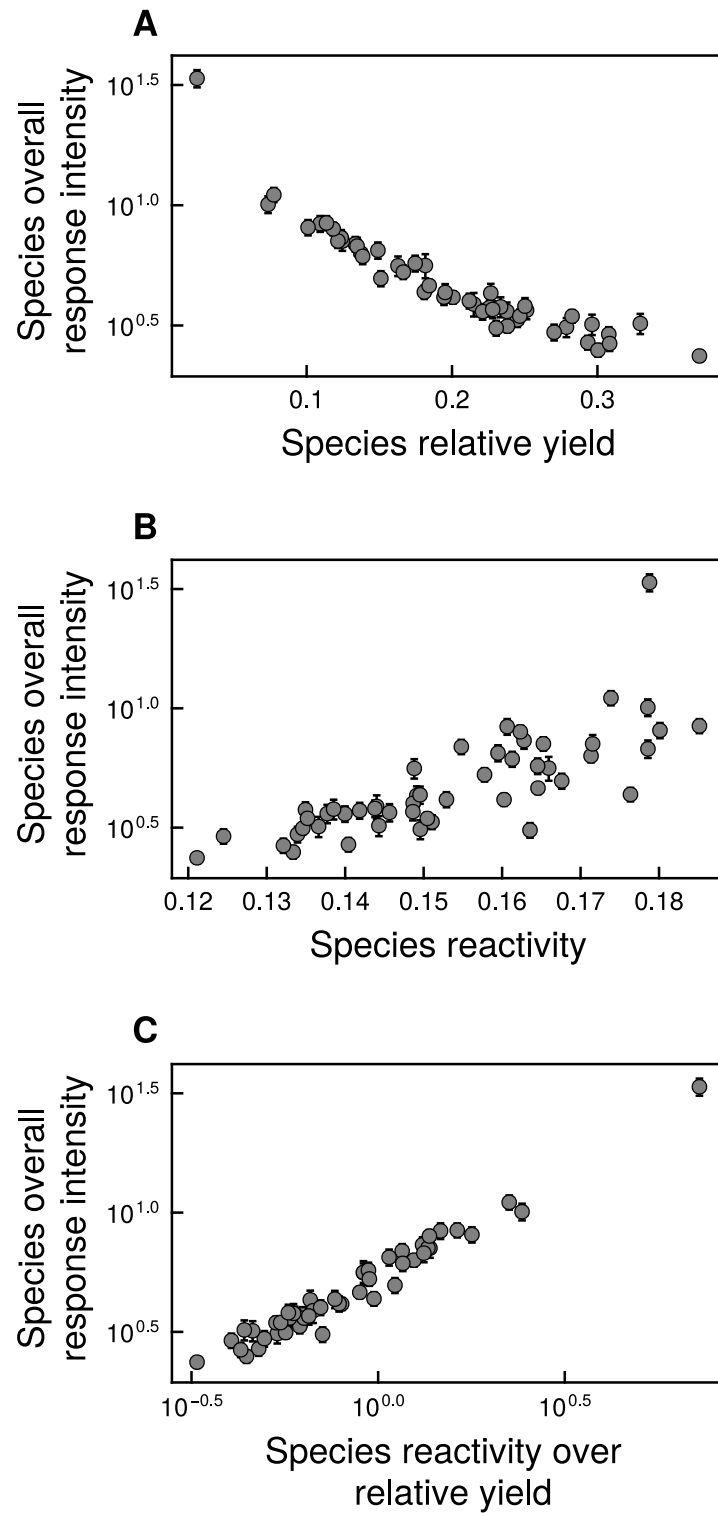


Figure S2. Species' overall responses to perturbations against species' resilience (A), reactivity (B) and their ratio (C). We assembled a community of $S = 50$ as described in the Material and Methods (Main text) and plotted the overall species' responses against their relative yield (resilience), their reactivity and the ratio of the two latter. Species predictability is averaged over 100 random perturbations. Error bars correspond to standard error.