Beyond biomass: how interactions shape species' importance for ecosystem functioning

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Abstract

Assessing the functional role of species in a changing world is critical for effectively preserving ecosystems. Intuitively, this role should relate to how the loss of a species impacts a function. We develop a general approach to define the functional contribution of a species that interacts with others. Using experimental data from a ciliate microcosm experiment, we infer species dynamic contribution based on the observed functional impact of their removal. Using both model simulations and empirical data, we demonstrate that dynamic contributions are generically unrelated to their biomasses and traits associated with the function, but rather reflect a species' overall effect on others, and the level of functioning in the community without that species. Our novel characterization of the functional contribution of species reveals that, due to biotic interactions, rare species that do not possess unique functional traits are just as likely as any other species to be functionally important.

Introduction

Understanding how ecosystems respond to global change is a central goal of functional ecology and conservation biology (Lavorel et al. 2002, Hong et al. 2022). In the context of the ongoing biodiversity crisis, it is crucial to assess how changes in community composition influence ecosystem functioning. Achieving this requires a deeper understanding of the roles species play in maintaining ecosystem functions.

Two important fields of research, functional ecology and Biodiversity and Ecosystem Functioning (BEF), have aimed at grasping the role of species with different approaches and conclusions. On the one hand, functional ecology posits that knowledge on traits at the species level (e.g. leaf area index, photosynthetic rate) captures the mechanisms structuring biodiversity and ecosystem functioning (Enquist et al., 2015; Lavorel and Garnier, 2002). The mass-ratio hypothesis introduced by Grime (1998) suggests that the immediate effect of a species on an ecosystem function is proportional to its biomass, in which case the functioning of ecosystems is

expected to be largely driven by the traits of dominant species. Accordingly, community-weighted trait means obtained from a snapshot of the community have generally been used to predict the impact of global changes on ecosystem functioning (Garnier et al., 2004). On the other hand, the BEF research field has consistently shown that species richness is a strong determinant of ecosystem functioning regardless of species identity, because species with different traits tend to occupy different niches and therefore to be functionally complementary to each other (Loreau et al. 2001; Loreau & Hector 2001; Hooper et al. 2005; Cardinale et al. 2007; Loreau et al. 2022). BEF implies that the contribution of species to ecosystem functioning largely depends on the ecological context in which species live, in particular on how they interact and partition resources. As a result, determining which species have a significant impact on ecosystem functioning is challenging (but see Jaillard et al., 2018). While the mass-ratio hypothesis and BEF are often opposed (e.g. Wasof et al. 2018; Smith et al. 2019; Brun et al. 2019), they are not necessarily contradictory, but a unifying perspective that assesses the importance of species in their ecological context is lacking.

The contrast between the mass-ratio hypothesis and BEF is blatant when it comes to assessing the role of rare species. Under the mass-ratio hypothesis, rare species are assumed to generally play a minor role in ecosystem functioning; they can only play a significant role in narrow ecosystem functions performed by species with highly uncommon functional traits. Understanding the functional role of rare species has driven the quest for unique traits in rare species (Mouillot et al., 2013). From the BEF perspective, species richness itself matters even for broad functions (e.g. biomass production). The rare species in BEF assemblages should therefore be of some importance to ecosystem functioning. Supporting this perspective, *in situ* and *in silico* removal experiments have shown that removing rare species largely affects ecosystem functioning (Heilpern et al. 2018; Delalandre et al., 2022; Leitao et al. 2016; Peltzer et al., 2009).

The main implicit difference between the mass-ratio hypothesis and BEF lies in the role given to ecological dynamics. The mass-ratio hypothesis focuses on the biomass distribution in a community at a given point in time, without considering the processes that have generated this distribution. For example, the total biomass of a community is indeed simply the sum of the biomass of all its constituent species. Yet, a dominant species does not always contribute positively to biomass production; its presence may instead suppress the growth of more productive species. A species that is rare today may have played a key role in the past, facilitating the establishment of a productive species (Law and Morton, 1996; Koffel et al., 2018). By manipulating the ecological context and monitoring species biomass over long periods of time, BEF experiments enable us to reveal the effects of ecological interactions. The two mechanisms yielding positive BEF relationships emerge at least partly from species interactions: niche partitioning and facilitation increase the complementarity effect, while competitive dominance may generate a positive selection effect (Loreau & Hector 2001). The end-result of a strong, positive selection effect is that dominant species perform most of the ecosystem function, a view that coincides with the mass-ratio hypothesis. However, BEF experiments show that the complementarity effect generally predominates, while the selection effect is often variable and weak on average (Loreau & Hector 2001; Cardinale et al., 2007) and decreases further over time (Fargione et al., 2006). Thus, the

contributions of species to ecosystem functioning cannot be understood without taking account of their interactions and dynamics.

Interactions between species result in indirect effects, feedback loops, and cascading events (Pichon et al., 2024; Harvey et al. 2017). A major challenge when considering interactions is whether regularities can emerge with complexity (Lajaaiti et al., 2025; Sanchez et al., 2023; Liautaud et al., 2019), or on the contrary if they result in an irreducible context dependency and unpredictability of most ecosystem properties. Increases in complexity generally leads to higher context-dependence (Zelnik et al., 2024). Although recent experimental findings by Sanchez et al. (2023) suggest that such regularities may emerge when considering the functional contribution of species, how to relate the existence of such regularities to interaction patterns remains an open question.

The purpose of this article is to illustrate that biotic interactions do shape the functional role of species. Our first objective is to define a partitioning of ecosystem functions into **dynamic contributions** of species. This partitioning quantifies the role played by species in the response of ecosystem functions to long-lasting changes. Crucially, it accounts for how biotic interactions shape species contributions. Our second objective is to compare the contribution of species as classically understood in functional ecology as a combination of functional (effect) trait and biomass (hereafter **static contribution**) to the dynamic contribution of species. We contrast the dynamic and static contribution of species in simulated and empirical communities from a ciliate microcosm experiment (Pennekamp et al., 2018). Our third objective is to understand how the pattern of a species' interactions with others determines its dynamic contribution to ecosystem functioning.

Methods

Defining a dynamic partitioning of an ecosystem function

To meet our first objective, we start from the mass-ratio hypothesis in which each species contributes to a function Φ according to its biomass N_i and its contribution per unit of biomass, i.e. effect trait t_{Ei} (as in Lavorel and Garnier, 2002; Violle et al., 2007; Heilpern et al., 2018).

$$\Phi = \sum_{i=1}^{S} t_{Ei} \times N_i = \sum_{i=1}^{S} \Phi_i^{stat} \quad (1)$$

In this partitioning of the ecosystem function, each species has a **static contribution** $\Phi_i^{stat} = t_{Ei} \times N_i$ which is observable at any moment in time, from a snapshot of the community. This decomposition applies to any function (eg. total biomass, nitrogen litter content, polymer degradation) as the units and values of effect traits change (Fig. 1b). Effect traits are species-specific attributes converting biomasses to the unit of the function. In what follows, we assume the effect trait to only depend on species identity. When the function is total biomass, all species have the same contribution per unit of biomass, and the unit of the function is the same as species

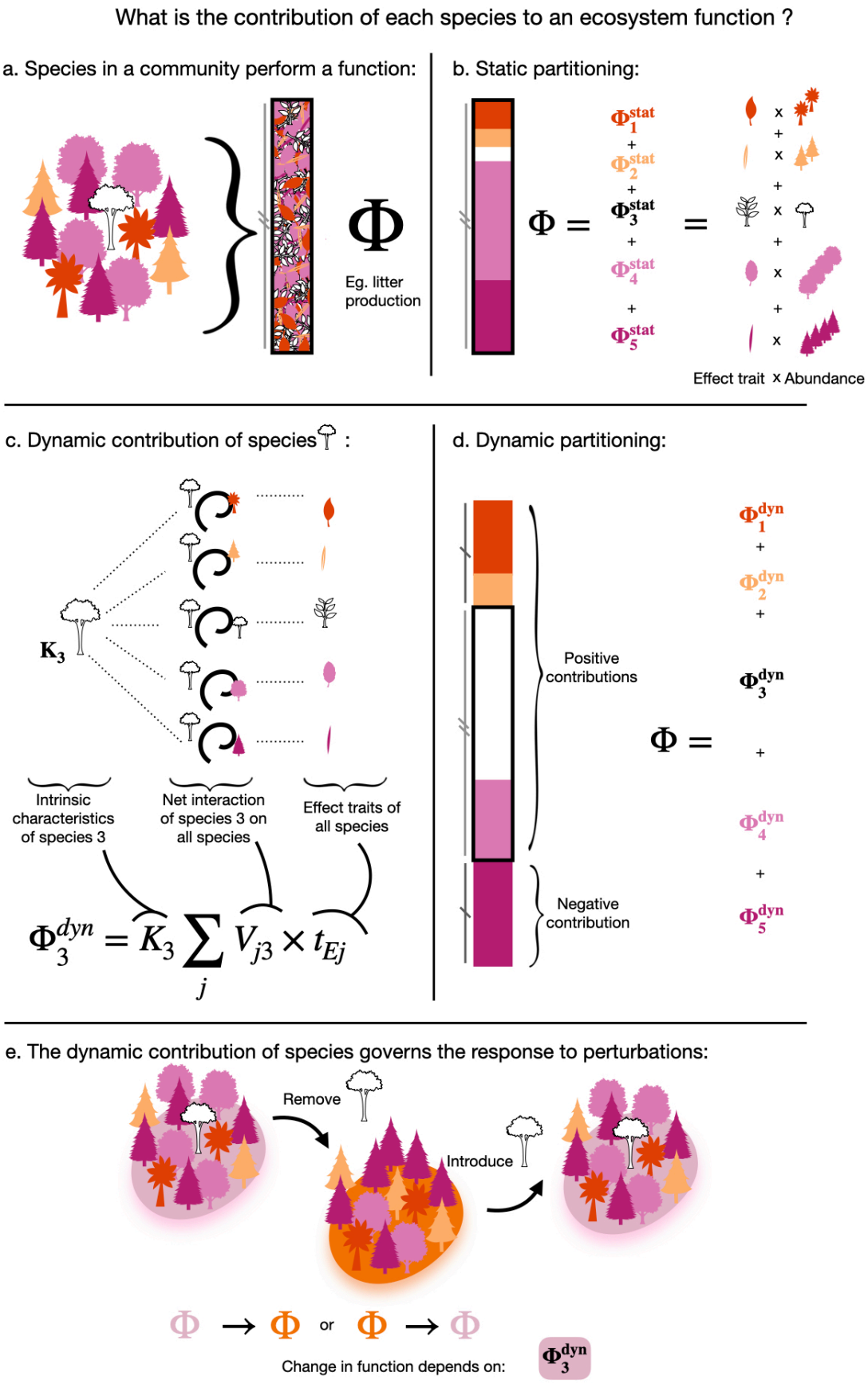

Figure 1: An ecosystem function can be partitioned into static (b) and dynamic (d) contributions of species. While the static contribution depends only on the traits and abundance of species, the dynamic contribution of one species links the effect trait of every other species to the intrinsic characteristic of the focal species via net interactions (c). The dynamic contribution captures the response of ecosystem functioning to perturbations such as extinctions or introduction of species (e).

biomass; all effect traits are 1 (dimensionless). If the function is nitrogen litter content [mg g^{-1}], the effect traits capture the species-specific amount of litter produced per unit of biomass and the N concentration of the produced litter, i.e. in units [mg g^{-2}]. The distribution of effect traits among species indicates whether a function is broad (ie. most or all species perform it, most or all species have a high effect trait) or narrow (i.e. only one or a group of species perform it, most species have an effect trait of 0). Although effect traits can be more or less density dependent—metabolism for instance (Fant and Ghedini, 2014) or enzyme production (Sanchez-Gorotsiaga et al., 2019), assuming constant effect traits is a useful starting point for our theory, and one that reflects the assumptions underlying the use of community weighted means in functional ecology. Furthermore Orr et al. (2024) have recently showed that considering functions as a sum of traits weighted by abundance is an accurate framework to reveal patterns in ecosystem multi-functional responses to global change.

However, this approach only *implicitly* considers the role of species interactions, which come into play as ecological dynamics unfold over time. Interactions between species influence their biomass, and thus their static contribution to functions. Our goal is to define a notion of functional contribution of species that *explicitly* accounts for ecological dynamics. We propose to construct a **dynamic partitioning** that reflects the sensitivity of a function to changes in intrinsic demographic parameters of species, such as their carrying capacities K_i, reflecting a species performance when alone in the environment:

$$\Phi_i^{dyn} = \frac{\partial \Phi}{\partial K_i} K_i^*. \qquad (2)$$

Here the coefficients K_i^* are uniquely defined such that, for any function,

$$\Phi = \sum_{i=1}^{S} \Phi_i^{dyn} \qquad (3)$$

By construction, the dynamic contribution of species predicts the response to any perturbation of the form $K_i \to K_i + \delta K_i$ (press perturbation). Indeed, the change in ecosystem functioning after a perturbation reads:

$$\delta\Phi = \sum_i \Phi_i^{dyn} \left(\frac{\delta K_i}{K_i^*} \right) \qquad (4)$$

Where $\delta K_i / K_i^*$ can be thought-of as the intensity of the perturbation affecting species *i*, and could be evaluated as the monoculture sensitivity.

Because $\partial\Phi/\partial K_i = \sum_j t_{E_j} \partial N_j / \partial K_i$, if we call $V_{ji} = \partial N_j / \partial K_i$ the net interaction (sum of direct and indirect interactions) from species *i* to species *j* (Zelnik et al. 2024), then (Fig. 1c):

$$\Phi_i^{dyn} = \sum_j \underbrace{t_{E_j}}_{\text{effect trait of species j}} \times \underbrace{V_{ji}}_{\text{net interaction of i on j}} \times \underbrace{K_i^*}_{\text{weight given to i}} \quad (5)$$

Where K_i^* is defined such that $\sum_i V_{ji} K_i^* = N_j$. Note that for Generalised Lotka-Volterra models, we have that $N_i = \sum_j V_{ij} K_j$ so that $K_i^* \equiv K_i$. Deviations between K_i^* and K_i will occur for community models departing from GLV dynamics.

The dynamic contribution of species encapsulates the sensitivity of a function to perturbations of species intrinsic demographic parameters (here carrying capacities, Eq. 2 and 4), and in doing so reveals the effect of net interactions between species. Eq. 5 emphasizes that the dynamic contribution of a species *i*, Φ_i^{dyn}, does not only depend on that species effect trait. For example, Φ_i^{dyn} can be large if, in the long term, species *i* facilitates (i.e. has a positive net interaction on) other species with large effect traits. On the contrary, the dynamic contribution of species *i* decreases if it suppresses in the long term (has a net negative net interaction on) species with strong effect traits. The static and dynamic contribution of species possibly have different values, and even different signs as the dynamic contribution of a species can be negative (e.g. purple species in Fig 1d).

Contrasting the dynamic and static contributions in empirical and simulated communities

Our next objective is to show that the static and the dynamic contribution are generically uncorrelated. To infer the dynamic contribution from empirical data, a next step is necessary. The dynamic contribution of a species can be obtained from the effect of a specific kind of press perturbation: the removal of a species. Indeed, the removal of a species is a targeted press perturbation that leads to the extinction of the focal species i: $K_i \to K_i + \delta K_i$ such that $V_{ii}\delta K_i = -N_i$ (Appendix A). Let $\Delta\Phi_i = \Phi - \Phi^{\backslash i}$ be the change in ecosystem functioning due to the removal of the species i from the community. We define this difference so that a positive value implies that the species has a net positive impact on the function in question, and thus that its removal is detrimental. Applying our dynamical partitioning (Eq. 4) to predict the effect of the perturbation $\delta K_i = -N_i/V_{ii}$ that pushes the species to extinction, effect of removing a species is directly linked to its dynamic contribution:

$$\Delta\Phi_i = \Phi_i^{dyn} \times \frac{N_i/V_{ii}}{K_i^*} \quad (6)$$

The term V_{ii} encodes the species sensitivity (Arnoldi at al 2022), and is uniform across species for disordered networks or when interactions are weak (Bunin 2017). Conversely, this means that the dynamical contribution of a species can be estimated from the effect of its removal in a given community:

$$\Phi_i^{dyn} \propto \frac{\Delta\Phi_i}{N_i} \times K_i^* \tag{7}$$

where the proportionality constant is the mean sensitivity. Since the sum of Φ_i^{dyn} is known (=Φ), so that dynamical contributions are relative notions to begin with, we do not need to know what this mean sensitivity precisely is.

We can note the occurrence in the above expressions of the ratio $\eta_i = N_i/K_i^*$ which is akin to the **relative yield** of species i. The relative yield is a notion rendered popular by the BEF literature (Loreau & Hector 2001), which captures the extent to which species *i*'s biomass is suppressed in a community ($\eta_i \ll 1$), benefits from living in a community ($\eta_i > 1$), or is on average unaffected by interactions in the community ($\eta_i \approx 1$).

With this approximation of the dynamic contribution of a species at hand, we analyzed data from an experimental ciliate community experiment (Pennekamp et al., 2018). Six species (*Tetrahymena, Colpidium, Dexiostoma, Loxocephalus, Paramecium, Spirostomum)* were grown at 53 different diversity levels during 57 days, with complete representation of the levels of richness 1, 2, 5 and 6. We focus on total biomass for which the effect trait of every species is 1. We show results from communities grown at 19°C.

Estimating biomass and interactions: After visual inspection of the time series of species abundances, we used the last 6 data points of the experiment, at which the biomasses approximately stabilized, and retrieved the mean biomass of each species in each community. We equated the carrying capacities to the biomasses in monoculture, and obtained the pairwise interactions from duo cultures and monocultures, such that $A_{ij} = (N_i^{(j)} - K_i)/N_j^{(i)}$. For all six species, we estimated their mean interaction effect $\overline{a_i} = \text{mean}(A_{ji}/K_j)$.

Obtaining the change in ecosystem function: We measured the change in total biomass due to the removal of a species by comparing pairs of communities which only differed by one species in their composition. For each species, we obtained 21 comparisons, yielding a total of 126 comparisons for the 6 species.

Simulations: We ran simulations of a generalized Lotka-Volterra model with S=9 species, where parameters were randomly drawn to showcase the genericity of our results. We integrated the differential equations with the DifferentialEquations package (v1.9.0, Rackauckas and Nie, 2017) in Julia (v1.10.4, Bezanson et al. 2017), until an equilibrium was reached (biomasses did not vary by more than 10^{-6} between two integration time steps). The carrying capacities and effect traits were drawn from a uniform distribution between 0.5 and 1 and 0 and 1 respectively. The mean interaction strength $\overline{a_i}$ was drawn between -0.9 and 0.5, and the deviation from mean interaction

Δa_{ij} drawn between -u_a and u_a, so that parameter u_a governs the heterogeneity of interactions (u_a close to 0 implies low variability in interactions while a large u_a implies variable interactions).

Understanding how the pattern of a species' interactions with others relates to its dynamic contribution

Our final objective is to demonstrate that the context-dependence of a species' dynamic contribution is shaped by patterns of species interactions. Two key aspects of these interaction patterns are the average (mean) and variability (variance) of a species' effect on other species. We further show that simple relationships can emerge between a species' dynamic contribution and the overall functioning of the community in its absence — a baseline we refer to as the **background level of functioning** ($\Phi^{\setminus i}$).

The dynamic contribution of a species Φ_i^{dyn} reads (see Appendix A for derivation):

$$\Phi_i^{dyn} = V_{ii}(t_{Ei}K_i^* + \Phi^{\setminus i}\overline{a_i}K_i^*) \tag{8}$$

In this expression, $t_{Ei}K_i^*$ is the level of ecosystem functioning in monoculture. The term $\overline{a_i}K_i^*$ can be interpreted as the weighted mean of $a_{ki} = A_{ki}/K_k^*$, the interactions incoming from species *i*. This weighted mean has to be understood with care since the weights are the relative dynamical contributions of affected species, and those contributions could be negative. If the interactions a_{ki} are homogeneous (i.e. not variable), the dynamic contribution of a species depends on its average effect on other species. A species that tends to facilitate all other species therefore has a positive dynamic contribution, and its contribution increases as the overall ecosystem functioning increases. A species that competes homogeneously with all others species has a declining dynamic contribution as the overall level of ecosystem functioning increases, such that its dynamic contribution may end up negative. If the interactions are heterogeneous (highly variable), an apparently facilitative species (i.e. one that facilitates most species present in the community) can have a negative effect on functioning if it facilitates a strongly antagonistic species (i.e. a species whose dynamical contribution is negative).

From Eq. 8, we therefore expect that when a species has an homogeneous effect (with a low variance) on others, its dynamic contribution should be linearly positively or negatively linked to the level of background functioning depending on the mean interaction effect. On the contrary, we expect that when a species has an heterogeneous effect (with a high variance) on others, its dynamic contribution is independent of background functioning. We test whether this relationship exists in empirical and simulated communities.

Results

In the section **Defining a dynamic partitioning of an ecosystem function**, we defined the dynamic contribution of species to an ecosystem function as the sensitivity of the function to

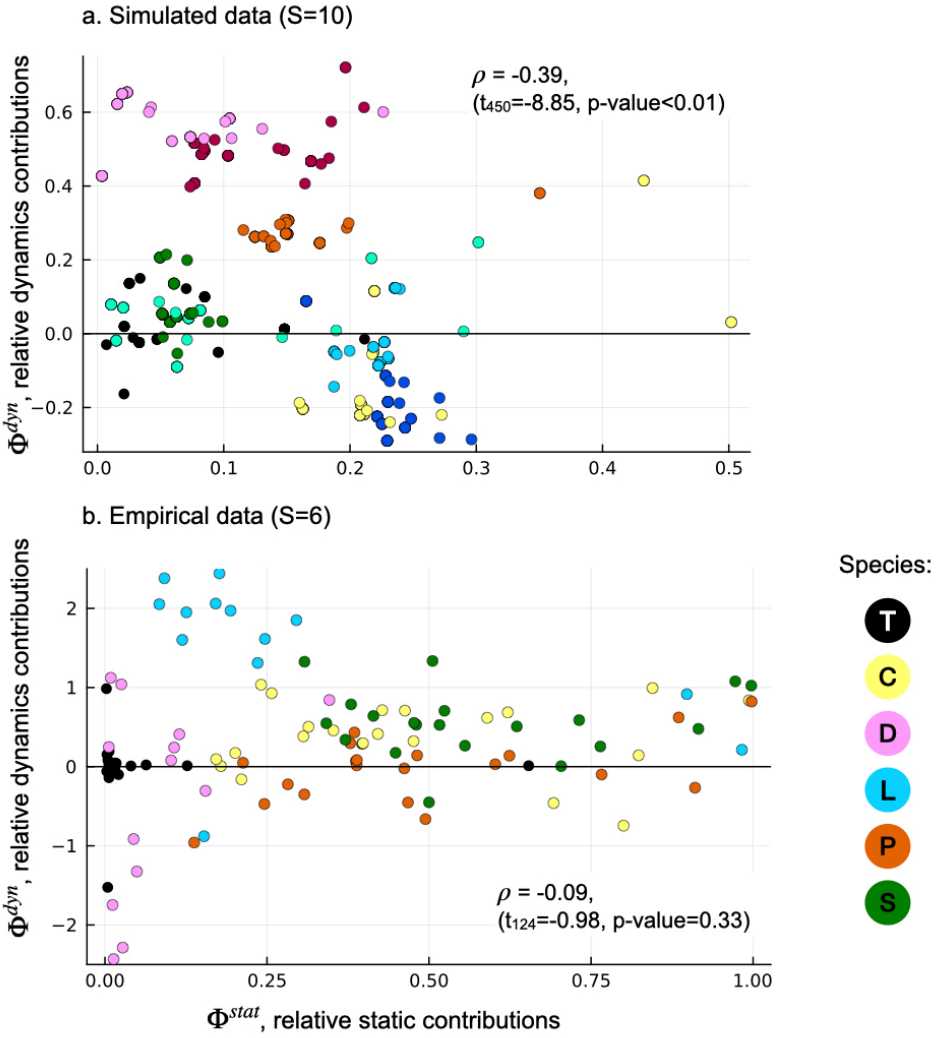

Figure 2: Dynamic contributions are not necessarily correlated to static contributions. Each dot corresponds to a species in a community, dots are colored by species. There are species that tend to have a low static contribution but a high dynamic contribution (eg. pink species in a., *Loxocephalus* in b), species with a high static contribution but a low dynamic contribution (eg. yellow species in a., *Loxocephalus*, *Paramecium* and *Spirostomum* in some communities is b.), and species whose dynamic contribution vary in sign (eg. black and aquamarine species in a., *Dexiostomata* in b.)

perturbations affecting that species. In a community, the sum of the dynamic contributions of all its constituent species add up to the ecosystem function (Objective 1).

In figure 2, we contrast the static and dynamic contributions of all species across biotic contexts (Objective 2), showing that they are not correlated in both simulations (Fig 2a) and empirical data (Fig 2b). On the right, dots correspond to species that are dominant (they have a high static contribution), but their vertical position shows that these species can both have a null dynamic contribution (all dots close to the black line), negative contributions (e.g. yellow and orange dots in b) or a strong positive contribution (e.g. yellow and orange species in 2a). On the contrary, on the left, dots correspond to species that are rare or lowly contributing the the

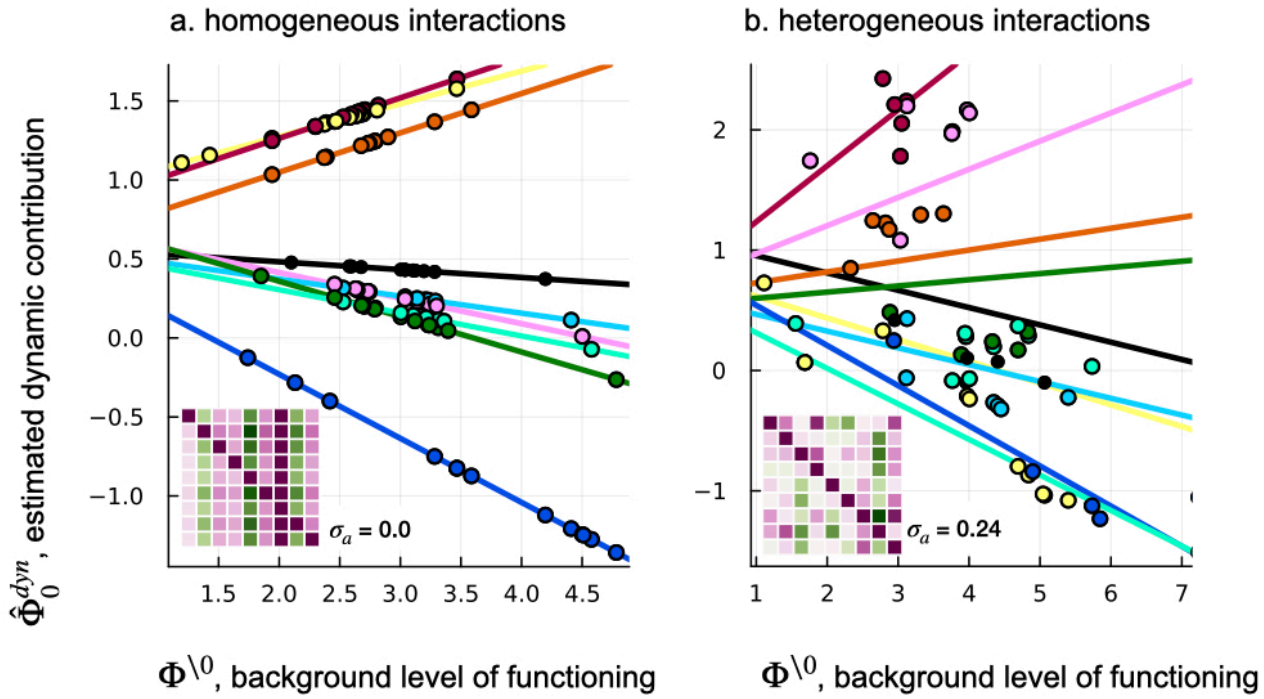

Figure 3: When the effect of the species on others is homogeneous (u_a = 0 resulting in a the standard deviation of interactions of σ_a=0.0), its dynamic contribution scales linearly with the level of functioning prior to the introduction $\Phi^{\backslash 0}$ (panel a). However, when the introduced species has an heterogeneous effect on others (u_a = 0.6 and σ_a=0.24), the relationship between the dynamic contribution and the background ecosystem functioning erodes (panel b).

function, but their vertical position indicates that they can have strongly positive dynamic contributions (e.g. pink species in 2a) or negative contribution (*Dexiostomata* in 2b).

In figure 4, we illustrate how species' interactions patterns (mean and variance of its effect on others) are reflected in their dynamic contributions across biotic contexts (Objective 3). Specifically, we show that background functioning and the mean effect of a species on others explains its dynamic contribution, when the variance in effect that that species has on others is low. Figure 3 illustrates the effect of the variance in simulations: when the variance of interactions is low (Fig. 3a), the dynamic contribution of species is explained by the level of background functioning and by the mean effect of that species (see how dots fall on the theoretical prediction). As the variance in interactions increases (Fig 3b), the relationship between the background functioning and the dynamic contribution fades. In the empirical data (Fig. 4), the relationship is strong for species *Colpidium*, *Paramecium*, and *Spirostomum,* which have the lowest variance in their effects on others (σ_a are low in Fig 4). By contrast, *Tetrahymena, Loxocephalus and Dexiostomata,* whose interactions are much more variable (see how on a single column of Fig. 4g, positive and negative values exist; this column-wise variability is reflected by high σ_a in Fig 4), showcase idiosyncratic dynamical contributions across biotic contexts, unrelated to background

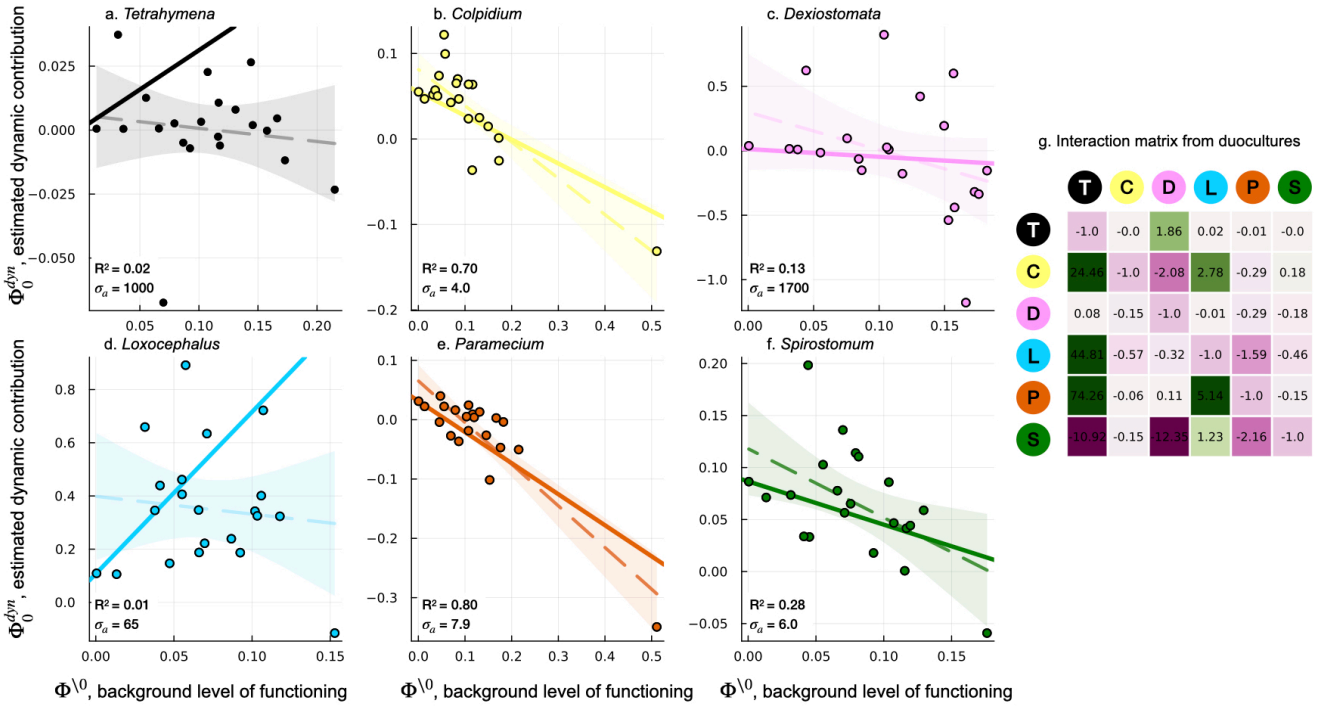

Figure 4: The dynamic contribution of some species is related to the background level of functioning, via the species's mean effect on other species. a-f: The solid line is the theoretical prediction from Eq. 8, while the dashed line is the statistical relationship between background functioning and the dynamic contribution, and the associated R^2 is on the bottom left of the panel. g: direct interactions (unscaled) between the 6 species in the communities. These direct interactions are scaled by the recipient species' carrying capacities to obtain the theoretical prediction in panels a-f. For 3 species, the statistical relationship closely aligns with the theoretical relationship (panels b, e and f). These species happen to have the most homogeneous effects on others, as shown by the low deviation in felt interaction σ_a of the three species. For the other three species, the dynamical contribution seems unrelated to the background level of functioning.

functioning. Our theory explains these inconsistent contributions as the result of complex indirect effects within the community where the species are introduced, resulting from high variability in species interactions.

Discussion

We introduced a new partitioning of an ecosystem function that takes into account biotic interactions and quantifies the role played by various species when a community responds to a long-term perturbation. We have shown that the dynamic contribution of species can be made operational by using several formulations, linking the dynamic contribution of species to the effect that that species' extinction would have, or to its average effect and the background level of functioning. When a species has homogeneous effects on others, its functional role can be simply described from both intrinsic characteristics of species —performance in monoculture, mean effect on others— and the ecological context in which it lives. Importantly, because of biotic interactions, the static and dynamic contributions are generically uncorrelated. This result demonstrates how the

mass-ratio hypothesis can be a valid static description of the role played by species in an ecosystem and yet be misleading when ecological dynamics come into play. Our results, which reflect a generic outcome of biotic interactions in communities, highlight the importance of preserving species that may not seem important for ecosystem functioning based on their effect traits and relative biomass alone.

Species dynamic contributions is shaped by biotic interactions, and as a result, depends on the biotic context in which a species exists. In the empirical data, species *Tetrahymena, Dexiostomata*, and *Paramecium* show, across communities, a dynamic contribution to total biomass whose sign varies. The variation highlights that depending on the baseline community in which they are present, removing them can either increase or decrease total biomass.

Furthermore, species dynamic contribution is governed by both biotic interactions and its intrinsic characteristics. In spite of its negative direct interactions with the other species, *Spirostomum* has a consistent positive dynamic contribution to community biomass. Because *Spirostomum* has a high biomass in monoculture —intrinsic characteristic of the species—, the negative relationship (due to negative direct effects) with the background ecosystem functioning is not sufficient to drag its dynamic contribution to negative values. However we would expect *Spirostomum* to have negative contributions in more productive ecosystems.

In other words, because species interact, their individual contribution to ecosystem functioning is a collective, context-dependent outcome. In particular, species can dynamically contribute to functions that they do not perform directly. Decades of BEF research have highlighted the context-dependency of species contributions to ecosystem functioning (Sandau et al., 2016; Bannar-Martin et al., 2018), yet using this context dependency to draw conclusions at the species level has rarely been attempted. Sanchez et al. (2023) made a step towards understanding the dynamical role of individual species in ecosystem functioning. Using microbial experiments and re-analyzing BEF data, they showed that the effect of introducing a species depends on the level of functioning prior to the introduction. The link between the dynamical contribution and net effects of a species provides a theoretical foundation for the empirical findings of Sanchez et al. (2023). We could decompose a species contribution in two terms, the first representing monoculture functioning, the second being the background functioning of the community multiplied by the mean direct interaction from the focal species. The second term therefore encodes context dependency. A major objective of functional ecology is to find measurable traits of organisms that can scale-up to correspond to effect traits of populations, expressed in units of the function per units of biomass (Lavorel and Garnier, 2002; Violle et al., 2007). Our work complements this research agenda by highlighting the role of biotic interactions in shaping the distribution of the biomass across species, and thus revealing species functional roles.

When a species is a general facilitator or competitor (i.e. the species has a similar effect on other species in the community), the effect of its introduction on ecosystem functioning is incremental: the level of functioning after the introduction of the species cannot be radically different from the functioning prior to its introduction - this dependency has been pointed out in previous work and is analogous to epistasis and the effect of a mutation (Sanchez et al., 2023; Diaz-Colugna et al., 2024). This finding resonates with Liautaud et al. (2019) who show that when

interactions show a low variance in the community, a small change in environmental conditions will lead to a small change in community composition. On the contrary, we show that when interactions are heterogeneous, the dynamic contribution of species can radically depart from its mean effect. The effect of its introduction is therefore less predictable and would require taking into account all the net interactions between that species and the resident species. We expect the relationship pointed out in Diaz-Colugna et al. (2024) and in Eq. A12 to erode as the analysis is reproduced in organisms that interact with higher variability among each other (e.g. a community in which the by-product of one bacteria can be used as a resource for some species while it is toxic to others).

Determining the dynamic contribution of species *in situ* or from experiments is challenging and requires sufficiently long times series. Our model simulations show that the dynamic contribution of species does not capture the response to disturbances at short timescales, i.e. before the ecological equilibrium is reached (see Appendix C). Since the effect of net interactions unfolds over long timescales (Brown et al., 2001; Montoya et al., 2009, Zelnik et al. 2024), determining the dynamic contribution of species requires that the biomass of species and ecosystem functions are monitored on sufficiently long timescales. While *in situ* time series are sometimes difficult to interpret due to multiple interacting factors (e.g. abiotic variations, direct and net interactions; Brown et al., 2001), analyzing long-term time series with the notion of dynamic contributions may improve our understanding of the complex responses of communities.

Rare species, whose functional role has notoriously been challenging to understand (Lyons et al., 2005), may contribute to ecosystem functions in the dynamic sense. When considering the static contribution of species, species can only have a high contribution if they are the only ones to contribute to a narrow function, i.e. they have a unique effect trait. Rare species uniquely contributing to functions have been identified in a variety of ecosystems (e.g. Mouillot et al. 2013 in coral reef fishes and tropical trees; Pester et al., 2010 in peatland microbial communities, Soliveres et al., 2016 in grasslands). In these cases, it is obvious that losing a rare species threatens the ecosystem function to which it contributes (O'Gordman et al. 2011). With our approach, we highlight, less intuitively, that rare species can also have a high contribution in the dynamic sense, via their interactions with other species. In plant communities, species of the genus *Equisitum* in wetlands or *Lupinus* in grasslands (Hinsinger et al., 2011; Marsh et al. 2000), for example, could have a high dynamic contribution. These two genera, though not abundant (5% of total biomass for *Equisitum*), increase the availability of phosphorous for *Lupinus* (Hinsinger et al., 2011, Jaillard et al., 2018), phosphorous, potassium and calcium for *Equisitum* (Marsh et al., 2000), thereby facilitating the species that end up being dominant. These rare species, via their interactions, are important in the dynamic sense. Their high dynamic contribution implies that ecosystem functioning is possibly threatened by the extinction of these rare species.

Consequently, static and dynamic contributions to ecosystem functioning have different implications for conservation. While conservationists may be tempted, in order to preserve a function or implement a restoration plan, to prioritize species based on their static contribution ecosystem functioning (Laughlin, 2014), with the notion of dynamic contribution, we explain why focusing on individual traits and biomass can misleadingly mask the importance of some species.

Species that highly interact with others are likely to have strong dynamic contributions (Soulé et al., 2003, Harvey et al., 2017).

Our dynamic partitioning should, by definition, predict the response of ecosystem functions to any type of perturbation that modifies the species intrinsic characteristics of species (e.g. a pesticide that reduces growth rates, habitat destruction reducing carrying capacities). Given that the dynamic contributions of species depends on interactions, and that the strength of interactions may vary with environmental context (Callaway et al., 2002; Piccardi et al., 2019; Koffel et al., 2018), predicting the response of an ecosystem function to a perturbation that also modifies interactions (e.g. temperature change, fertilization) is more subtle.

To conclude, our approach reveals, why, in some instances, the mass ratio-hypothesis and its applications (such as community-weighted means) may fail to grasp the actual contribution of species to ecosystem functioning. Due to its interactions with other species, a species typically has a dynamic contribution that differs from its static contribution. The notion of dynamic contribution is particularly relevant in a changing world since it has more predictive power than the static contribution of species. Long-term experiments or observations, monitoring biomasses at the species level after one or more disturbances, are necessary to infer the dynamic contribution of species in nature.

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Appendix A: from net effects to dynamic contributions, and relationship with background functioning

We start from our definition of the net effect of species i on ecosystem functioning:

$$\Delta\Phi_i = \Phi - \Phi^{\backslash i} \qquad \text{A1}$$

Noting $\delta N_j = N_j - N_{j/i}$ the change in the biomass of species j as a consequence of the presence of species i, where $\delta N_i = N_i$ by definition, the net effect on functioning reads:

$$\Delta\Phi_i = \sum_j t_{Ej}\delta N_j \qquad \text{A2}$$

Removing species *i* amounts to perturbing its carrying capacity enough to push the species to extinction. Assuming linearity, this perturbation $-\delta K_i$ can be computed as

$$\delta N_i = \frac{\partial N_i}{\partial K_i}\delta K_i = V_{ii}\delta K_i = N_i \qquad \text{A3}$$

This specific perturbation impacts other species as well, and at linear order

$$\delta N_j = V_{ji}\delta K_i = V_{ji}K_i^* \times \frac{N_i/K_i^*}{V_{ii}} \qquad \text{A4}$$

We can then obtain the change in ecosystem functioning resulting from changes in the biomass of all species:

$$\Delta\Phi_i = \frac{N_i/K_i^*}{V_{ii}}\sum_j t_{Ej}V_{ij}K_i^* = \frac{N_i/K_i^*}{V_{ii}}\Phi_i^{dyn} \qquad \text{A5}$$

Where we recognized the expression of Φ_i^{dyn} from its derivation Eq. 7 of the main text.

We can manipulate the expression of Φ_i^{dyn} further to obtain another expression in which the background level of functioning $\Phi^{\backslash i}$ appears. The idea is to note that species i acts as a perturbation on the community formed without it. This perturbation directly amounts to a change $\delta K_k = A_{ki}N_i$ of the carrying capacity of any species *k*. Thus, noting $a_{ki} = A_{ki}/K_{k/i}^*$, we may write, still assuming linearity, that the shift in biomass of any given species *j* is:

$$\delta N_j = \sum_{k\neq i}\frac{\partial N_{j/i}}{\partial K_k}K_{k/i}^* a_{ki}N_i \qquad \text{A6}$$

With that in mind, we can now note that

$$\Phi_i^{dyn} = t_{E_i}\frac{\partial N_i}{\partial K_i}K_i^* + \sum_{j\neq i} t_{E_j}\frac{\partial N_{j/i}}{\partial K_i}K_i^* + \sum_{j\neq i} t_{E_j}\frac{\partial \delta N_j}{\partial K_i}K_i^* \qquad \text{A7}$$

The second term in the r.h.s. vanishes because $N_{j/i}$ does not depend on K_i. For the last term we can use the expression of δN_j just derived. We get to

$$\sum_{j\neq i} t_{E_j} \frac{\partial \delta N_j}{\partial K_i} K_i^* = \frac{\partial N_i}{\partial K_i} K_i^* \sum_{k,j\neq i} t_{E_j} \frac{\partial N_{j/i}}{\partial K_k} K_{k/i}^* a_{ki} = \frac{\partial N_i}{\partial K_i} K_i^* \sum_{k\neq i} \Phi_{k/i}^{dyn} a_{ki} \quad \text{A8}$$

Where we recognized the dynamical contributions of species in the community *without* species *i.* If we denote $\Phi_i^* = t_{E_i} K_i^*$, which we may think of as the functioning of a monoculture of *i*, then we get to

$$\Phi_i^{dyn} = V_{ii}(\Phi_i^* + \sum_{k\neq i} \Phi_{k/i}^{dyn} a_{ki} K_i^*) \quad \text{A9}$$

Because $\sum_{k\neq i} \Phi_{k/i}^{dyn} = \Phi_{/i}$ —the background functioning of the community without species *i*—

then we may simplify the expression further and recognize Eq. 8 in the main text:

$$\Phi_i^{dyn} = V_{ii}(\Phi_i^* + \Phi_{/i} \overline{a_i} K_i^*) \quad \text{A10}$$

Where the term $\overline{a_i} K_i^*$ can be interpreted as the weighted mean of the interactions incoming from species *i*. This weighted mean has to be understood with care since the weights are the relative dynamical contributions of affected species, and those contributions could be negative. This will not matter if the interactions a_{ki} are uniform, but could possibly reverse some expectations, making an apparently facilitative species have a negative effect on functioning if it facilitates a strongly antagonistic species (i.e. whose dynamical contribution is negative).

We can go back to the expression of the net effect $\Phi_i^{dyn} \eta_i / V_{ii}$ and deduce:

$$\Delta \Phi_i = t_{E_i} N_i + \sum_{k\neq i} \Phi_{k/i}^{dyn} a_{ki} N_i \quad \text{A11}$$

Because $\sum_{k\neq i} \Phi_{k/i}^{dyn} = \Phi_{/i}$, we can then simplify:

$$\Delta \Phi_i = \Phi_i^{stat} + \Phi_{/i} \overline{a_i} N_i \quad \text{A12}$$

The dependence between the response of ecosystem functioning and the background functioning has been empirically found in microbial communities (Sanchez et al., 2023).

Appendix B

Using simulations, we assessed whether the dynamic contribution of species could be estimated from Eq. 7, making the simplifying assumptions that the pseudo relative yield $\eta_i^* = N_i/K_i^*$is close to the actual relative yield $\eta_i = N_i/K_i$, and that the net auto-interaction effect is uniform:

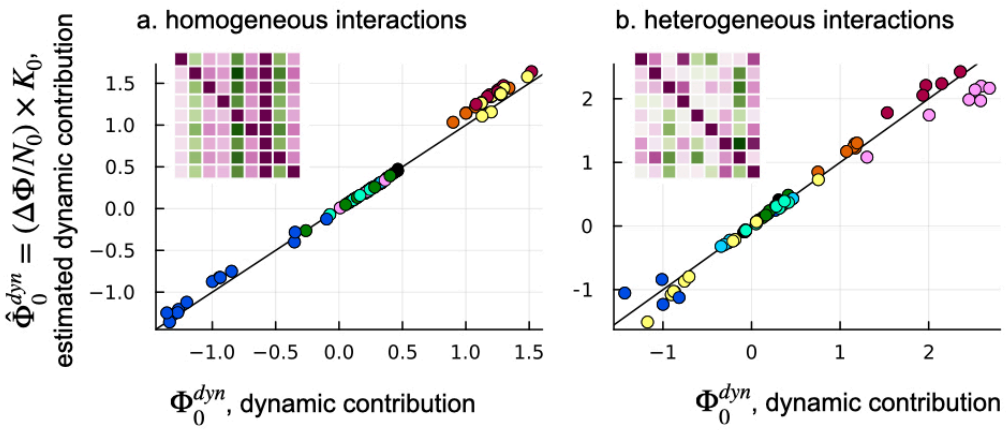

Figure B1: the dynamic contributions of a species $\Phi_0^{dyn} = \sum_j t_{Ej} V_{j0} K_0^*$ (exact expression from Eq. 5) can be estimated from the effect of introducing it in the community $\Delta\Phi_0$ and its relative yield η_0 . The prediction is accurate whether species have an homogeneous effect on others (u_a = 0) or an heterogeneous effect (u_a = 0.6).

Simulations show that the change in ecosystem functioning and the relative yield can be used to estimate the dynamic contribution of species, using Eq. 7 (Fig. B1). The relationship holds when the effect of species on others is homogeneous or heterogeneous: see how, in the interaction matrix in the top left of the panels, the columns are of the same color indicating a uniform effect of the column species on others in a, while in b, the same species can have both positive and negative effects on others, and of strongly varying magnitudes.

Appendix C: Short-term community responses are predicted by Φ^{stat}, while long-term responses are predicted by Φ^{dyn}

In this Appendix, we highlight the importance of timescales. Here, using simulations where we know the dynamic contribution of species, we ask whether the dynamic contribution can be used to accurately describe the response of the function to the extinction of a species. Specifically, we contrast the responses on the short-term and the long-term. $\Delta\Phi^{t}_{obs}$ was computed from ecosystem functioning obtained at short, middle and long term, i.e. until t=0.1, 1, and when species had reached their equilibrium biomasses respectively. Fig. C1 shows that in the very short term (first line), the ecosystem function changes by exactly the static contribution of the species (left panel). On the contrary, over long timescales, the effect of the extinction of a species can only be predicted from the dynamic contribution of the species, not from its static contribution (third roe). These findings suggest that while short-term experiments may corroborate mass-ratio point of views, making long-term predictions requires to take interactions between species into account.

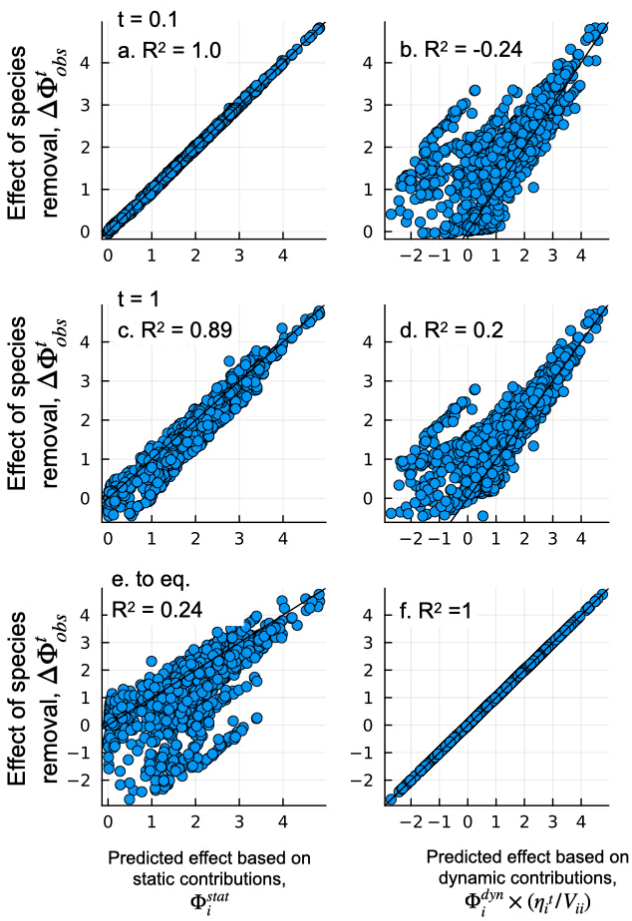

Figure C1: Effect of species removal at short (a and b), middle (c and d) and long (e and f) timescales. In the short term, the static contributions of species capture effectively the change in ecosystem functioning due to the extinction of the species (a).