Revealing the organization of species stability in ecological communities

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Abstract

Ecological communities are often composed of many species, each interacting in complex ways. This complexity makes predictions of species responses to disturbances challenging. Here, we analyze dynamical community models and reveal an unexpectedly simple principle: species stability is governed by a single metric—self-regulation loss (SL). SL quantifies the importance of self-regulatory processes in species' population dynamics. In effect, SL captures a collective outcome of species interactions, organizing how individual species respond to disturbances. When applied to data from protist community experiments, SL accurately forecasts species responses to temperature changes. Our work reveals that despite the complexity of ecological systems species stability follows a remarkably simple organizing principle.

Introduction

Species do not live in isolation: they eat, facilitate and compete with one another [1, 2]. Ecological communities consist of vast interaction networks that differ in size, number of links, and structure [3]. These interaction networks strongly influence the population dynamics of the species that form the community [4, 5]. For instance, predators feed on herbivores, herbivores deplete plants, and plants compete with one another for limited resources, such that, over ecological time scales, interactions between species mold how biomass flows throughout the community [6].

Within communities, species dynamics are not only influenced by direct interactions but also by indirect effects and feedback loops [7, 8]. For instance, plants depleted by herbivores may benefit indirectly from predators that suppress these herbivores. As interaction networks grow in complexity, indirect effects become increasingly intertwined, eventually reaching a point where the community's influence on individual species can no longer be understood as a simple sum of direct and indirect interactions [9]. This cohesiveness in community behaviour can produce unpredictable outcomes—rendering species responses to disturbances difficult to decipher [10, 11].

Traditionally, studies in functional ecology have focused on intrinsic species response traits—such as tolerance, avoidance or regeneration—to understand population stability [12, 13]. For example, researchers have linked generation times to demographic resilience across numerous taxa [14, 15, 16]. By contrast, community ecology studies have focused on how interspecific interactions shape the stability of entire communities [17]. Theoretical frameworks like random matrix theory [18, 19, 20] and structural stability theory [21, 22, 23] have provided significant insights into community-level stability. However, this focus on the community level often overlooks the variability in species-specific stability [24]. Consequently, the gap between studies that use trait-based approaches to explain stability at the species level and studies that focus on interspecific interactions across entire communities has resulted in a limited understanding of how biotic interactions influence the stability of individual species populations.

Uncovering what drives differences in the responses of species within the same community is critical for understanding the mechanisms underpinning community stability. Studies adopting this perspective have shown that compensatory dynamics can play a key role [25, 26]. For instance, in plant communities characterized by uneven abundance due to competition for resources, declines in dominant species following disturbances such as droughts are often offset by rare subordinate species benefiting from competition release [27, 28]. These findings highlight the importance of interspecific interactions in stabilizing communities and raise a fundamental question: Is there a universal principle organizing species stability across communities, or are these stability patterns so context-dependent that the search for regularities is bound to remain vain?

Although recent work suggests that species stability is linked to their competitive ability [29, 30], this relationship is highly context-dependent. The outcome

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depends on the features of the perturbation: in some cases, compensatory dynamics enhance the stability of subordinate species through competitive release, whereas in others, these dynamics fail, making dominant species more stable [29]. These findings point to an underlying principle governing species stability within communities. A principle that appears to manifest differently depending on the features of the perturbation (e.g., whether it triggers compensatory dynamics). However, the nature of this principle, its role in shaping stability responses, and whether it exists as a general organizing framework for species stability in complex communities remain largely unexplored.

Here, starting from a theoretical analysis of dynamical community models, we ask three key questions: (1) Is there a principle that organizes species individual responses to perturbations in complex communities? (2) What stability patterns are expected to emerge from this principle, depending on features of perturbations? And finally, (3) can we validate these predictions using experimental data?

Building on these questions, we developed a novel theoretical framework that reveals the principle organizing species stability across complex communities. Our theory reveals the central role of the self-regulation loss (SL), a metric which that quantifies the importance of intrinsic self-regulation in species responses. In the generalized Lotka-Volterra (gLV) model, this metric coincides with the relative yield (RY) [31], making it easy to measure. By integrating theory, simulations and experimental data, our approach not only forecasts the emergence of distinct stability patterns under various disturbance regimes but also reveals an unexpected simplicity in the organization of species stability. In the following sections, we present our findings, first introducing our theoretical framework and its application to a generalized Lotka-Volterra (gLV) model, and ultimately using it to predict species responses to temperature change in a ciliate community experiment [32].

Results

To study the stability of species within ecological communities, we consider a gLV model. The dynamics of species biomass (B_i) is given by

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_i B_i \left(1 + \frac{-B_i + \sum_{j \neq i} a_{ij} B_j}{K_i}\right) \qquad (1)$$

Within a community, species interact with one another through interspecific interactions (a_{ij}), which can be either positive (e.g., facilitation) or negative (e.g., competition). When studying the stability of species near a fixed point, the linear interactions can

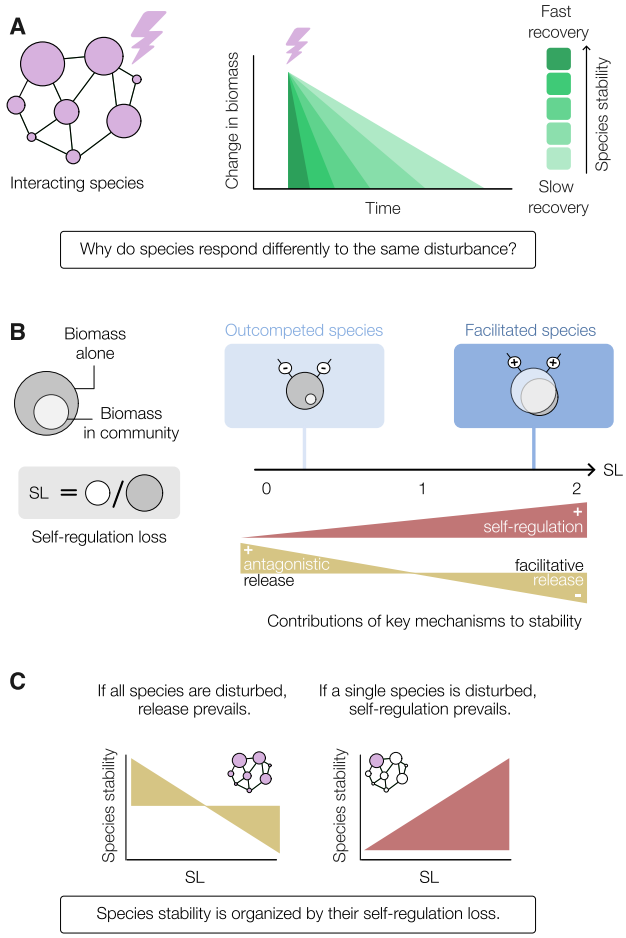

Figure 1: Conceptual illustration of how the self-regulation loss (SL) metric organizes species stability. (A) A disturbance (shown here as a pulse) is applied to a community of interacting species, triggering a community-wide response that can be viewed as the sum of individual species' responses. Some species rebound quickly, while others recover more slowly, prompting the question: What drives this variability in species responses? (B) We introduce the SL metric to quantify a species' self-regulation (i.e., intraspecific competition). Species with low SL lose biomass to competition, while those benefiting from facilitation exhibit high SL. When the entire community is perturbed, low-SL species may gain stability through antagonistic release as their competitors decline, whereas high-SL species can suffer from the loss of facilitative interactions. At the same time, as SL increases, self-regulation plays a greater role in promoting recovery. Here, self-regulation should be understood as an emergent community property rather than an intrinsic feature; for instance, species with SL greater than one rely on facilitative interactions to maintain stability. (C) Depending on the nature of the disturbance, either antagonistic release or self-regulation may dominate. When a disturbance targets a single species, antagonistic release should be negligible, because the competitors remain largely unaffected. Consequently, self-regulation prevails, favoring species with high SL. In contrast, community-wide disturbances affect all species simultaneously, promoting antagonistic release and thereby stabilizing species with low SL. Across these scenarios, species stability is systematically organized by their SL.

be thought of as local approximations of more complex interaction terms—such as non-linear or higher-order interactions. We consider that species can survive alone, and that their biomass when alone is given by their carrying capacity (K_i). For the clarity of our manuscript, we perform the analytical derivations assuming similar generation times for all species, $r_i = 1$, but relax this assumption in the Methods.

The stability of large communities is strongly determined by the mean and the standard deviation of interactions strengths [33]. To generate communities where a large number of species (S) coexist stably, we draw interspecific interactions in a Gaussian distribution centered in $\frac{\mu}{S}$ and with a standard deviation of $\frac{\sigma}{\sqrt{S}}$. This scaling allows us to choose and to generate stable communities with many species (Methods).

Self-regulation loss

When a community of interacting species experiences a disturbance, individual species often respond in variable ways—even when the disturbance impacts all species equally (Fig. 1A). A key source of this variability is how species dynamics are shaped by interspecific interactions. Yet, interactions are numerous rendering their effects hard to disentangle. We approach this task by deriving analytical expressions of species responses to disturbances (Methods). These derivations reveal a key term that appears to govern species responses: self-regulation loss (SL). SL measures the biomass loss due to self-regulation relative to intrinsic growth. In the gLV model, this metric simplifies to the ratio of a species' biomass in the community to its biomass in isolation, aligning with the classic concept of relative yield (RY) [34] (Fig. S1).

$$\mathrm{SL}_i = \frac{B_i}{K_i} \tag{2}$$

SL is determined by a species' intrinsic characteristics, through its carrying capacity, and by its biotic environment that shapes its biomass in the community. Species experiencing strong negative interactions exhibit low SL, as their biomass in the community remains small relative to their biomass in isolation. Conversely, species benefiting from strong facilitation can surpass their carrying capacity, leading to SL values greater than one. This reasoning applies to species with positive intrinsic growth that can persist in isolation, though our framework can be extended to include obligate dependent species (Fig. S4).

Since both intra- and interspecific regulatory forces underpin species stability, SL provides insight into how species respond to disturbances (Fig. 1B). A species with low SL experiences strong negative interactions—such as competition or predation—from the rest of the community, which reduces its equilibrium biomass. As a result, if the biomass of other species decreases, the focal species' biomass is expected to increase due to antagonistic release, i.e., a reduction in the net negative effects that suppress its biomass. Conversely, a species with SL greater than one maintains its equilibrium biomass through facilitative interactions with the rest of the community. Because of this reliance, a decline in other species' biomass is expected to lead to a decline in its own biomass as well. Between these two cases, species with SL close to one exhibit minimal dependence on the biomass fluctuations of other species. This can occur either because they interact weakly with others or because the positive and negative effects they receive from the community balance each other out. Regardless of the underlying process, such species are expected to be relatively unaffected by changes in the biomass of other species.

Recent findings further indicate that patterns of species stability vary with the extent of the disturbance—whether it targets a single species or affects the entire community [29]. We show that the SL metric is key to decipher these patterns (Fig. 1C). For targeted disturbances affecting only a single species, self-regulatory dynamics dominate, meaning that antagonistic release is minimal, and species with low SL tend to be less stable than species with high SL. In contrast, disturbances that affect the entire community can trigger strong antagonistic release effects,cenhancing the stability of species with low SL. In the following, we further explain how SL organizes species' responses to long-lasting changes in environmental conditions (hereafter a 'press disturbance') and instantaneous biomass removal (hereafter a 'pulse disturbance').

Response to press

Single-species press We modelled press disturbances by altering species carrying capacities. Following a press disturbance, species biomass shifts, and the magnitude of this change reflects the species' sensitivity to the disturbance. We define sensitivity as the ratio of the relative change in biomass observed in a community to the change if the species was alone (Methods). In this way, our measure captures how interspecific interactions influence the species' stability and we further ensure a fair comparison among species.

In the gLV model, species biomass changes in response to a press disturbance writes

$$\Delta B_i = \sum V_{ij} \Delta K_j \tag{3}$$

where V is the sensitivity matrix, obtained by inverting the interaction matrix (Methods). We first considered the simplest scenario, where only a single

species, i, is affected by the press. In this setting, the absolute change in biomass following the press simplifies to a single term: $\Delta B_i = V_{ii} K_i$. Moreover, in large, disordered communities with sufficiently weak interactions, the diagonal elements of the sensitivity matrix tend to be close to one ($V_{ii} \simeq 1$; Supplementary Materials, Fig. S3). We then wrote the expression of species sensitivity (s_i defined as the ratio of relative change in biomass and the relative change in carrying capacity, which yields

$$s_i^{\text{single}} = \frac{1}{\text{SL}_i} \tag{4}$$

To test this prediction (Eq. 4), we assembled a large generalized Lotka-Volterra (gLV) community and measured each species' SL before applying any disturbance. We then proceeded by applying targeted disturbances on each species successively and measured their resulting sensitivity. Our prediction (Eq. 4) closely matched observed species sensitivity (Fig. 2B).

The decrease in species sensitivity as the inverse of their SL emerges because the absolute change in a species' biomass within a community closely tracks the shift in its carrying capacity induced by a press disturbance. In other words, the press itself is not directly buffered or amplified by interactions; rather, interactions shape a species' biomass, which in turn determines its sensitivity. Species with an SL of one experience similar changes in biomass both in isolation and within the community, resulting in a sensitivity close to one. A species whose biomass is suppressed by antagonistic interactions will experience a proportionally greater loss within the community, leading to a sensitivity greater than one. Conversely, a species whose biomass is enhanced by facilitative interactions will exhibit a smaller loss in the community, resulting in a sensitivity lower than one. However, we expect these patterns to vanish when a press affects multiple species simultaneously, as the interplay of interspecific interactions further influences species stability.

Community-wide press While targeted disturbances affect a single species, environmental changes often impact entire communities. We next sought to extend our findings to the community-wide press. To achieve this, we considered that all species were affected by the press disturbance. Under this scenario, species sensitivity is also shaped by the response of others, which is captured by the interspecific terms of Eq. 3. By using a mean-field approximation (Methods) and considering the expected sensitivity over many disturbances, we obtain

$$s_i = \frac{1}{\text{SL}_i} + (1 - \frac{1}{\text{SL}_i})\langle \overline{\kappa_j} \rangle \langle \frac{1}{\kappa_i} \rangle \tag{5}$$

where $\langle \cdot \rangle$ denotes the expected value on the set of disturbances, $\overline{\kappa_j}$ the average press intensity taken on

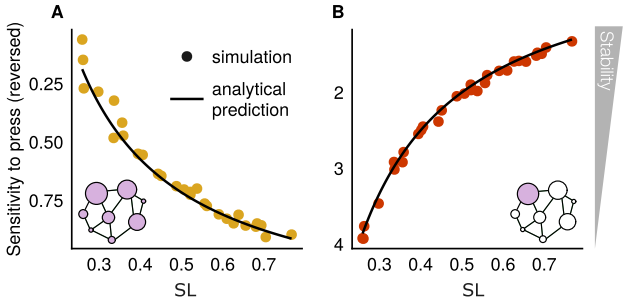

Figure 2: Species' self-regulation ratio (SL) organizes their stability to press disturbances. (A) Sensitivity of species to community-wide press perturbations, where the press is applied simultaneously to all species (Methods). Sensitivities are averaged over 1,000 disturbance events. Analytical prediction is given by Eq. 5. (B) Sensitivity of species to single-species press perturbations, where the press is applied to one species at a time (Methods). Sensitivities are averaged over 50 disturbances per species. Analytical prediction is given by Eq. 4. Note that sensitivity-axis is reversed so that upper points indicate greater stability, such that stability patterns are consistent with Fig. 1C.

all species except species i, and κ_i the press intensity on species i. Remarkably, the net impact of the community on species sensitivity can be expressed as a simple function of SL.

The key insight is that a species' response to disturbance is shaped not only by its own dynamics, captured by s_i^{single}, but also by its interactions within the community. Species with lower SL values are less stable under targeted press than species with higher SL. However, under a community-wide press, the strong antagonistic pressure experienced by low-SL species leads to a greater antagonistic release following the disturbance, ultimately enhancing their stability. Indeed, we observe that antagonistic release buffers species' biomass loss, as reflected in sensitivity values below one. In contrast, high-SL species experience a release of facilitative interactions, which hampers their stability.

The reverse phenomenon occurs for species with SL values greater than one (Fig. S4). Because these species rely on facilitative interactions to sustain their biomass, a community-wide press induces a facilitative release that weakens their stability. Facilitative release, the counterpart of antagonistic release, amplifies biomass loss, which is reflected in sensitivity values greater than one.

For the antagonistic release to prevail, the disturbance must impact other species sufficiently; specifically, when $\langle \overline{\kappa_j} \rangle \langle \frac{1}{\kappa_i} \rangle > 1$. This condition is typically met when disturbances affect all species similarly, as in this setting arithmetic mean exceeds harmonic mean (that is, $\langle \kappa \rangle \langle \frac{1}{\kappa} \rangle > 1$). Consequently, community-wide press disturbances reverse the sensitivity—SL relationship observed under targeted disturbances (Fig. 2A).

Response to pulse

Having established that the SL structures species stability under press disturbances, we next sought to find whether these findings extend to pulse disturbances—sudden, temporary shifts in species biomass. We quantified species stability through their recovery rate, which describes how quickly species return to equilibrium after the disturbance (Methods).

We studied the recovery of species relative deviation around their equilibrium, $z_i = \frac{B_i - B_i^{\mathrm{eq}}}{B_i^{\mathrm{eq}}}$. To do so, we linearized the dynamics (assuming small deviations), and we used a mean-field approximation similar as the one performed for press disturbance (Methods). This simplifications reduces the recovery dynamics to two key components

$$\frac{1}{z_i}\frac{\mathrm{d}z_i}{\mathrm{d}t} = -\mathrm{SL}_i + (1 - \mathrm{SL}_i)\frac{\overline{z_j}}{z_i} \tag{6}$$

The first term reflects the species' ability to recover as if it was the only species perturbed, that is, its characteristic recovery rate. The second term captures the contribution of the community to the species stability. High-SL species benefit from strong self-regulation, while low-SL species gain stability from interspecific interactions—provided that the disturbance affects the species they interact with. These two mechanisms echo those we previously identified for press disturbances.

Using an approach similar to [35], we solved Eq. 6 to derive the expected recovery trajectories over a large set of pulse disturbances. This analysis revealed broad, recurring patterns across disturbances, notably uncovering two distinct phases of recovery (Fig. 3A). Immediately following a pulse disturbance, species with low SL recover rapidly due to antagonistic release triggered by the decline of their suppressors. This rapid recovery, however, is followed by an overshoot of equilibrium biomass—as these species reach equilibrium while still benefiting from antagonistic release. As the community approaches equilibrium and interspecific effects wane, intrinsic resilience takes over, ultimately favoring species with high SL.

This behavior is captured quantitatively by examining species' short- and long-term average recovery rates (Methods). In the short term, species with low SL recover faster because of antagonistic release (Fig. 3B). Over longer time scales, however, the advantage of antagonistic release diminishes, and species with high SL—benefiting from strong self-regulation—recover more rapidly (Fig. 3C).

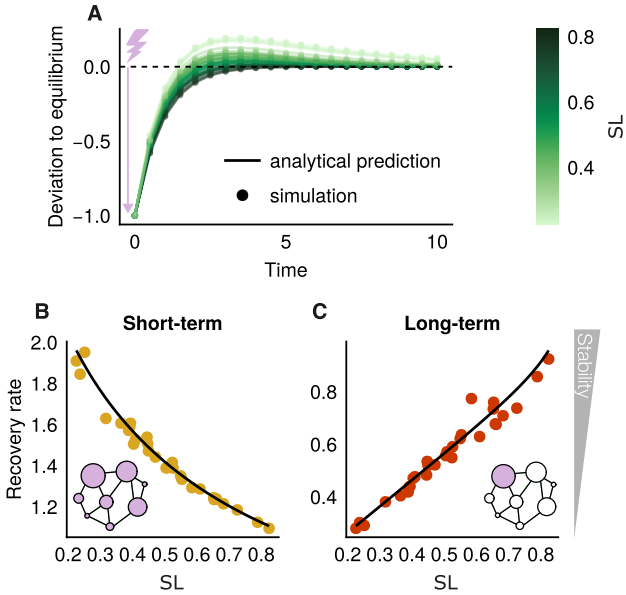

Figure 3: Species' SL organizes their recovery to pulse disturbances. (A) Species recovery trajectories over time. Trajectories are averaged across 5,000 random pulse perturbations (Methods). Deviation to equilibrium is defined as $\frac{\Delta B_i(t)}{\Delta B_i(0)}$ with $\Delta B = B_i - B_i^{\mathrm{eq}}$, normalized so all species start at a value of -1. Over time, species return to equilibrium, with the deviation approaching 0. Analytical prediction is given by Eq. 9 (Methods). (B) Short-term return rate vs. SL. The return rate is averaged over the interval $t = 0$ to $t = 1$. The network indicates that in the short-term all species are far from their equilibrium, making the link with the stability pattern observed for community-wide press (Fig. 2A). (C) Long-term return rate vs. SL. The return rate is averaged over the interval $t = 0$ to $t = 10$. Networks do not reflect the initial extent of the disturbance, as shown in Fig.2; in both cases, the pulse affects all species. However, they illustrate that in the short term, all species deviate significantly from equilibrium, whereas in the long term, only a few have not recovered, linking this pattern to the stability responses observed in single-species press disturbances (Fig.2B).. Averages are computed over 1,000 random pulses. Analytical prediction for the recovery rates is given by Eq. 10 (Methods).

Case study

We next tested the applicability of our framework on experimental data. We reanalyzed time series data from [32], which monitored ciliate communities over 57 days. These communities were assembled with varying species compositions (ranging from one to six species) and were exposed to a temperature gradient from 15 to 25°C.

In our analysis, we defined the press disturbance as the temperature change that alters species biomass both in isolation and within the community (Fig. 4B,C). We observed a linear relationship between species biomass in the community (averaged on all community combinations) and their carrying capacity, which validates a key assumption of our framework.

We further estimated the sensitivity of each species in each community composition by fitting a linear model on their biomass in this community and their carrying capacity, across the range of temperatures

studied (Methods). As we were able to measure species carrying capacity, we also inferred species SL in these communities. As a result, we obtained how species sensitivity to temperature change depends on their SL in each community composition. We tested our analytical predictions (Eq. 5) against these data. Remarkably, our prediction closely captured the observed species sensitivities to temperature change (Fig. 4A).

We observed that a given species can exhibit varied SL, showing how different community compositions and therefore interspecific interactions, shape its SL. Importantly, the variability in species sensitivity is well-captured by its SL—demonstrating that species sensitivity is not solely the result of its intrinsic properties (e.g. a life-history trait) but is also shaped by the community it lives in.

We observed ciliates with SL values largely exceeding one, indicating the presence of facilitative interactions (e.g., Dexio in Fig. 4A). However, our prediction works well across the entire range of observed SL, demonstrating that the mechanisms it captures are not limited to fully competitive communities but also apply to communities with more diverse interactions. Specifically, our framework explains the higher sensitivity (lower stability) of species with high SL due to the destabilizing effects of facilitative interaction release, while low-SL species gain stability from antagonistic release. Together, these findings highlight that our framework successfully identifies key mechanisms driving species stability within real ecological communities.

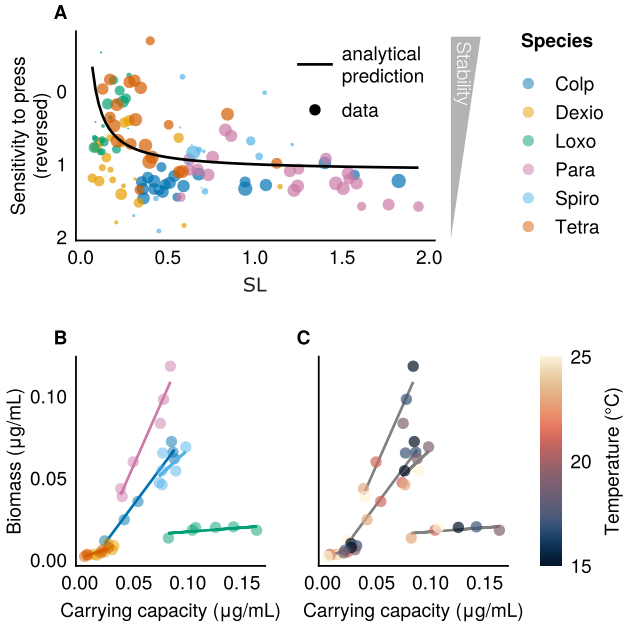

Figure 4: Predicting response of ciliate communities to temperature change. (A) Species sensitivity to temperature change against their SL, with the analytical prediction based on Eq. 5 (Methods). Point sizes decrease with the size of the confidence interval. (B) Species average biomass in community against their carrying capacity colored by species. (C) Same plot but colored by temperature to show the impact of temperature on species biomass and carrying capacity. As temperature increases, both parameters tend to decrease.

Discussion

Understanding how interspecific interactions shape species stability is a threefold challenge. First, interactions are numerous, and their effects on species dynamics are often complex and difficult to decipher—especially in tightly integrated communities where indirect effects and feedback loops can render species responses to disturbances unpredictable [9, 11, 10]. Second, it is practically challenging to measure all pairwise interactions within a community [36, 37], assuming that pairwise interactions still make sense when considering more than two species [38, 39]. Third, species stability is highly context-dependent and may not exhibit consistent patterns across different communities.

Here, we demonstrate that the challenge of understanding species stability in complex communities can be addressed using a single metric applied at the species-level: self-regulation loss (SL). This metric captures the balance between two key mechanisms promoting stability: self-regulation, which reflects a species' ability to counteract deviations from equilibrium density, and compensatory dynamics, which arise through antagonistic release. We note that the importance of self-regulation is governed by SL, which in turn depends on a species' equilibrium biomass—reflecting its biotic environment while remaining independent of the underlying processes that shape it. A species can exhibit high SL either due to weak interactions, making it largely independent of others, or because facilitative interactions offset negative ones. While this abstraction loses information about specific processes, it enhances predictability—allowing SL to reliably capture species responses to disturbances, regardless of the processes at play.

Intuitively, species benefiting strongly from facilitation sustain high densities, implying great loss due to self-regulation (SL $\gtrsim$ 1). In contrast, species maintained to low densities by antagonistic interactions—such as competition or predation—exhibit small self-regulation loss (SL $\ll$ 1) and can benefit greatly from the release of antagonistic interactions when their suppressors decline. Because the SL metric captures the combined effects of both effects, compensatory dynamics and self-regulation, we show that species stability is systematically organized along this axis. Overall, our findings demonstrate that, despite the complexity of ecological communities, fundamental

mechanisms driving stability can be disentangled and understood within a unified framework.

One of our key findings is an analytical condition predicting when the stabilizing effect of antagonistic release outweighs self-regulation, marking the onset of compensatory dynamics [25]. When disturbances reduce species biomass, they alleviate antagonistic pressures such as competition or predation, which in turn buffer individual species' biomass—and, by extension, total community biomass—against loss. According to our theory, because antagonistic release depends on the decline of a species' suppressors, it does not emerge when a disturbance targets a single species. In contrast, disturbances affecting the entire community should promote antagonistic release. These predictions align with recent findings showing that compensatory mechanisms arise in response to community-wide disturbances but not to species-specific ones [29]. Furthermore, climate change experiments in plant communities have demonstrated that rare, subordinate species can increase in biomass following environmental stress (e.g., drought) due to the decline of dominant competitors, thereby buffering overall community biomass loss [27, 40]. Together, these results highlight the stabilizing role of compensatory dynamics in ecological communities.

In the case of community-wide pulse disturbances, where the perturbation is not maintained over time, we predict that the influence of interaction release (antagonistic or facilitative) will diminish as the system recovers, giving way to self-regulation as the primary driver of species recovery. For example, if a fixed fraction of biomass is removed from all species, suppressed species initially experience a strong antagonistic release due to the decline of their suppressors, allowing them to recover rapidly. By contrast, facilitated species undergo facilitative release, which hampers their recovery. However, as species recover antagonistic and facilitative interactions return. At this point, species recovery rate equates their SL, marking the disappearance of interaction release. Previous studies have noted a disconnection between short- and long-term recovery phases of communities [41, 42, 43], for instance by comparing community reactivity (i.e., short-term amplification of a disturbance) to community resilience (i.e., asymptotic return rate). Theoretical work suggested that abundant species contribute to community reactivity and govern the short-term recovery, while rare species contribute to community resilience and the long-term recovery [35]. We further show that the differences in the contributions of rare and abundant species to reactivity and resilience is explained by the transition between two distinct recovery processes. In the short term, species respond to the release of interspecific interactions, experiencing either antagonistic or facilitative release depending on the prevailing interaction type. In contrast, the long-term stabilization of the community is governed by self-regulation.

Alongside compensatory dynamics, we found self-regulation to be a key mechanism governing species and community stability. Self-regulation is known to be essential for stable species coexistence [44, 18]. Dynamical models often require high levels of self-regulation to generate stable yet diverse communities, as observed in nature [45, 46]. However, our results indicate that at the level of individual species, stronger self-regulation does not always equate to greater stability. In particular, species with high SL " benefit less from antagonistic release and can even suffer from facilitative release, which hampers their stability when $\mathrm{SL} \geq 1$, as their high biomass is maintained by their biotic environment. This highlights the nuanced role of self-regulation in species stability, where the balance between biotic interactions and internal dynamics determines a species' ability to recover from disturbances.

By identifying two key mechanisms that contribute to species stability—antagonistic (or facilitative) release and self-regulation—that operate across various disturbance types, our work bridges previously disconnected facets of ecological stability. Stability is indeed a multifaceted concept, defined and measured in many ways [47, 24], which has often led to conflicting interpretations. One species or community may appear more stable than another according to one metric yet less stable according to another [32, 24]. While previous studies have attempted to link different stability measures [48, 49, 50, 51], they have largely focused on community-level stability and relied on correlative approaches, offering limited mechanistic insights. In contrast, our approach connects different dimensions of stability through a mechanistic understanding of individual species responses. We found that species sensitivity to community-wide press disturbances and short-term recovery from pulse disturbances are both governed by antagonistic release, while species sensitivity to targeted press disturbances and long-term recovery are determined by self-regulation. Because these pairs of metrics are controlled by the same underlying mechanisms, they exhibit similar patterns and high correlations. In this way, our theory provides a robust foundation for understanding the mechanisms linking seemingly unrelated stability metrics.

SL can be conceptually divided into two distinct notions that are confounded in the gLV model (Supporting Information, Fig. S1): a timescale ratio and a biomass ratio. The timescale ratio determines the characteristic speed of recovery following a pulse disturbance, while the biomass ratio—which can be seen as a generalized form of RY—captures the extent to

which a species' biomass is suppressed by antagonistic interactions and, consequently, the stability it gains through antagonistic release. In the gLV framework, these two aspects collapse into a single metric, RY, which enables (i) a straightforward measurement of species SL as a simple biomass ratio and (ii) the unification of species responses to both press and pulse disturbances under the same predictive framework. However, when species dynamics become nonlinear—for instance, when growth follows a sublinear scaling [52]—these two components decouple, and their relationship can even become negative. Despite these subtleties, species stability follows a clear organization—even in more complex models—that provides a basis for predicting species responses to disturbances (Supporting Information, Fig. S1).

Although our study focuses on species-level stability to develop a mechanistic understanding of the underlying principles, most research measures stability at higher organizational levels [24], such as entire communities. This raises an important question: do the patterns we observe at the species level simply scale up, or do species-level differences cancel each other out when aggregated?

Previous studies on temporal variability have shown that strong competition reduces population stability by amplifying fluctuations in species biomass. However, this decline in species-level stability does not necessarily lead to lower stability of total community biomass, as increased competition also enhances asynchrony, counterbalancing individual fluctuations [53, 54]. We observe a similar phenomenon in our framework when examining community responses to pulse and press disturbances (Supporting Information, Fig. S2). Stronger competition leads to higher species stability, as the stability gain from antagonistic release increases with competition strength. However, at the community scale, this stabilizing effect vanishes, as the contribution of antagonistic release wanes when aggregated across all species. As a result, community stability remains largely unaffected by competition strength. This example highlights how stability patterns at the species level can disappear when considered at the scale of the entire community.

One limitation of our study is that we have focused on species that can survive in isolation (e.g. autotrophs). This allowed us to simply measure their SL as the ratio of their biomass within a community to their biomass when alone. However, many species depend on interactions with others to persist—a plant may require facilitation to endure harsh conditions, or a consumer may depend on its prey. We refer to these as "dependent species". For them, we extend the SL metric by comparing self-regulation to intrinsic mortality instead of intrinsic growth, and our initial numerical results suggest that this extended SL effectively organizes their stability (Supplementary Information, Fig. S4). Nevertheless, two key challenges remain. First, accurately measuring self-regulation in dependent species in experimental settings is difficult, and rarely done. Second, because dependent species rely on obligate positive interactions, they may exhibit unique stability mechanisms that are yet to be explored. Addressing these challenges through targeted experiments and refined models is a natural next step.

In conclusion, our study reveals that species stability in ecological communities is organized by a surprisingly simple principle. By disentangling the main forces regulating species populations, we provide new insights into the mechanisms driving species responses to disturbances. Although challenges remain, particularly regarding the experimental measure of species self-regulation and the mechanistic understanding of its origins, our work lays a robust foundation for future research aimed at predicting community responses to environmental change. We show that an emerging simplicity does exist in species-rich ecological communities, a hopeful omen that useful scientific knowledge can exist at this level of organization.

Methods

Derivation of species response to press

To study species stability within complex communities, we consider a generalized Lotka-Volterra (gLV) model, where species biomass dynamics follow

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_i B_i \Big(1 + \frac{-B_i + \sum_{j\neq i} a_{ij} B_j}{K_i}\Big).$$

At equilibrium, species biomass satisfies

$$B_i^{\mathrm{eq}} = K_i + \sum_{j\neq i} a_{ij} B_j^{\mathrm{eq}}. \tag{7}$$

In the absence of interactions, species biomass in the community equals their carrying capacity. However, as interaction strength increases, species biomass becomes increasingly shaped by the biotic environment, breaking its correlation with intrinsic carrying capacity [9]. By rearranging Eq. 7, we isolate the carrying capacity:

$$K_i = -\sum_j a_{ij} B_j^{\mathrm{eq}},$$

where $a_{ii} = -1$. In vector form, this equation reads

$$\mathbf{K} = -\mathbf{A}\mathbf{B}^{\mathrm{eq}},$$

where $\mathbf{K}$ is the vector of species carrying capacities, $\mathbf{B}^{\mathrm{eq}}$ is the equilibrium biomass vector, and $\mathbf{A}$ is the

interaction matrix. Defining the sensitivity matrix as $\mathbf{V} = -\mathbf{A}^{-1}$, we can express equilibrium biomass as

$$\mathbf{B}^{\mathrm{eq}} = \mathbf{V}\mathbf{K}. \tag{8}$$

Now, we introduce a press disturbance, modeled as a change in carrying capacity given by the vector $\Delta\mathbf{K}$. The resulting change in equilibrium biomass follows

$$\Delta\mathbf{B}^{\mathrm{eq}} = \mathbf{V}\Delta\mathbf{K}.$$

To quantify how biotic interactions influence species stability, we define species sensitivity to press disturbances as the ratio of its relative biomass change in the community to its relative biomass change in isolation. This definition ensures a fair comparison across species with different biomasses or carrying capacities. Biomass changes in isolation and in the community are given by

$$\left(\frac{\Delta B_i^{\mathrm{eq}}}{B_i^{\mathrm{eq}}}\right)_{\mathrm{alone}} = \frac{\Delta K_i}{K_i}, \quad \left(\frac{\Delta B_i^{\mathrm{eq}}}{B_i^{\mathrm{eq}}}\right)_{\mathrm{com}} = \frac{\sum_j V_{ij}\Delta K_j}{B_i^{\mathrm{eq}}}.$$

Taking their ratio, species sensitivity is given by

$$s_i = \frac{V_{ii}}{\mathrm{SL}_i} + \frac{1}{B_i^{\mathrm{eq}}}\frac{1}{\kappa_i}\sum_{j\neq i} V_{ij}K_j\kappa_j,$$

where $\kappa_j = \frac{\Delta K_j}{K_j}$ denotes the press intensity, and species self-regulation is defined as $\mathrm{SL}_i = \frac{B_i^{\mathrm{eq}}}{K_i}$.

In disordered communities where interactions are weak enough to permit stable coexistence, the diagonal elements of the sensitivity matrix are approximately equal across species and close to one, $V_{ii} \simeq 1$ (Supporting Information, Fig. S4). To further simplify, we adopt a mean-field approximation, assuming that press intensities κ_j are weakly correlated with $V_{ij}K_j$. This assumption holds when disturbances are proportional to species carrying capacity, i.e., $\Delta K_j \propto K_j$, leading to

$$s_i = \frac{1}{\mathrm{SL}_i} + \frac{1}{B_i^{\mathrm{eq}}}\frac{\overline{\kappa_j}}{\kappa_i}\sum_{j\neq i} V_{ij}K_j,$$

where $\overline{\kappa_j}$ is the average press intensity across species except i. Using Eq. 8 for species i, we obtain the final expression for species sensitivity:

$$s_i = \frac{1}{\mathrm{SL}_i} + (1 - \frac{1}{\mathrm{SL}_i})\frac{\overline{\kappa_j}}{\kappa_i}.$$

Taking the expected sensitivity across many press experiments yields Eq. 5.

Derivation of species responses to pulse

We now focus on species responses to pulse disturbances, which we model as an instantaneous perturbation in biomass, $x_i = B_i - B_i^{\mathrm{eq}}$. Assuming small deviations from equilibrium, we linearize the system around B_i^{eq}, leading to the species recovery equation, normalized by its generation time r_i^{-1} as suggested by [55]:

$$\frac{1}{r_i}\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\frac{B_i^{\mathrm{eq}}}{K_i}x_i + \sum_{j\neq i}\frac{a_{ij}}{K_i}B_i^{\mathrm{eq}}x_j.$$

Introducing species self-regulation loss (SL) and the relative biomass deviation $z_i = \frac{x_i}{B_i^{\mathrm{eq}}}$, we obtain

$$\frac{1}{r_i}\frac{\mathrm{d}z_i}{\mathrm{d}t} = -\mathrm{SL}_i z_i + \sum_{j\neq i} a_{ij}\frac{K_j}{K_i}\mathrm{SL}_j z_j.$$

To focus on interactions shaping species coexistence, we define core interactions as $a'_{ij} = a_{ij}\frac{K_j}{K_i}$ [56]. These rescaled interactions are the relevant terms for species coexistence and are drawn randomly to generate communities with a high number of coexisting species.

Following a mean-field approximation as before, we assume weak correlations between $a'_{ij}\mathrm{SL}_j$ and z_j, a reasonable assumption in species-rich communities, where initial perturbations $z_j(t=0)$ are drawn from a distribution independent of species interactions. This simplifies the equation to

$$\frac{1}{r_i}\frac{\mathrm{d}z_i}{\mathrm{d}t} = -\mathrm{SL}_i z_i + \overline{z_j}\sum_{j\neq i} a'_{ij}\mathrm{SL}_j$$

where $\overline{z_j}$ denotes the mean species deviation. Using Eq. 7 (divided by K_i), we simplify the sum to

$$\sum_{j\neq i} a'_{ij}\mathrm{SL}_j = \mathrm{SL}_i - 1.$$

Substituting this into the previous equation gives the simplified differential equation governing species recovery (Eq. 6):

$$\frac{1}{r_i}\frac{1}{z_i}\frac{\mathrm{d}z_i}{\mathrm{d}t} = -\mathrm{SL}_i + (\mathrm{SL}_i - 1)\frac{\overline{z_j}}{z_i},$$

To explicitly solve this equation, we first derive the trajectory of the average species deviation, $\overline{z_j}$. In species-rich communities, we assume that $\overline{z_j} = \overline{z}$, the mean deviation over all species, including i. It can then be shown that the trajectory of $\overline{z}$ follows a simple exponential decay:

$$\overline{z} = \overline{z(0)}e^{-\overline{r}t},$$

where $\overline{r}$ is the average species growth rate. This allows us to express the recovery trajectory of species i:

$$\frac{z_i(t)}{z_i(0)} = e^{-r_i\mathrm{SL}_i t} + \frac{\overline{z(0)}}{z_i(0)}\frac{1-\mathrm{SL}_i}{\frac{\overline{r}}{r_i} - \mathrm{SL}_i}(e^{-\overline{r}t} - e^{-r_i\mathrm{SL}_i t}).$$

Taking the expected value over multiple disturbances [35], denoted by $\langle\cdot\rangle$, and assuming $z_i(0)$ follows

a common distribution with arithmetic and harmonic means $\langle z_0 \rangle$ and $\langle \frac{1}{z_0} \rangle^{-1}$, respectively, we obtain

$$\frac{\langle z_i(t) \rangle}{\langle z_0 \rangle} = e^{-r_i \mathrm{SL}_i t} + \langle z_0 \rangle \langle \frac{1}{z_0} \rangle \frac{1 - \mathrm{SL}_i}{\frac{\bar{r}}{r_i} - \mathrm{SL}_i} (e^{-\bar{r}t} - e^{-r_i \mathrm{SL}_i t}). \tag{9}$$

From this, we derive the expected species average recovery rate between 0 and t:

$$R_i(t) = -\frac{1}{r_i t} \log \left(\frac{\langle z_i(t) \rangle}{\langle z_0 \rangle} \right). \tag{10}$$

where $z_i(t)$ is given by Eq. 9. This full expression underpins our analytical predictions, but further approximations allow for better interpretation. In the short term, the recovery rate simplifies to

$$R_i^{\mathrm{short}}(t) \simeq -\mathrm{SL}_i \Big(1 + \langle z_0 \rangle \langle \frac{1}{z_0} \rangle (\frac{1}{\mathrm{SL}_i} - 1) \Big).$$

This demonstrates that species SL dictates two fundamental aspects of species recovery: their characteristic recovery timescale and the strength of antagonistic release. Specifically, we observe that a species' recovery rate is proportional to its SL. Additionally, the term capturing antagonistic release is proportional to $\frac{1}{\mathrm{SL}_i} - 1$, meaning it is large when $\mathrm{SL}_i \ll 1$ and vanishes when $\mathrm{SL}_i = 1$. However, in nonlinear models where SL is no longer equivalent to RY, these two recovery features are not solely controlled by SL (Fig. S1). While the characteristic recovery rate remains governed by SL, antagonistic release is instead determined by RY.

In the long term, antagonistic release vanishes, leaving only species characteristic recovery rate to govern their recovery:

$$R_i^{\mathrm{long}}(t) \simeq -\mathrm{SL}_i.$$

Simulations

We simulated communities of $S = 30$ species. Following previous studies [56, 33], we draw core interspecific in Gaussian distributions $a'_{ij} \sim \mathcal{N}(\frac{\mu}{S}, \frac{\sigma}{\sqrt{S}})$, with $\mu = -1$ and $\sigma = 0.3$. Furthermore, $a_{ii} = -1$ in our parametrization as self-regulation is already captured by species carrying capacity K_i, that are drawn in a Gaussian distribution $K_i \sim \mathcal{N}(1, 0.3)$. To center on the effect of interspecific interactions on species stability, we took $r_i = 1$ for all species. Press intensities were drawn in $\kappa \sim \mathcal{D}$, and pulse disturbances in $z_0 \sim \mathcal{D}$ for all species. Simulations were run in the Julia programming language [57] using the DifferentialEquations package [58].

Data

We analyzed data from a previously published experiment [32], which factorially manipulated temperature (15, 17, 19, 21, 23, and 25 °C) and species richness (1–6 species) in assemblages of bacterivorous ciliates: *Colpidium striatum* (Colp), *Dexiostoma campylum* (Dexio), *Loxocephalus sp.* (Loxo), *Paramecium caudatum* (Para), *Spirostomum teres* (Spiro), and *Tetrahymena thermophila* (Tetra). Species biomasses were measured over a period of 57 days.

We estimated species carrying capacity (K_i) by regressing species biomass against community richness. Specifically, we defined K_i as the predicted biomass at richness = 1, allowing us to leverage the entire dataset. This regression was performed using the GLM package in Julia [59].

To quantify species sensitivity in the experiment, we expressed it as:

$$s_i = \frac{B_i^{\mathrm{eq}}}{K_i} \frac{\Delta K_i}{\Delta B_i^{\mathrm{eq}}}.$$

Here, K_i represents the mean carrying capacity observed across all temperatures, while B_i^{eq} is the equilibrium biomass of species i across temperatures for each community composition. To minimize transient effects, we restricted analyses excluded the first seven time points from the time series. Moreover, we considered communities with at least three species.

The second term, $\frac{\Delta K_i}{\Delta B_i^{\mathrm{eq}}}$, was estimated as the slope of a linear model relating species biomass in communities to their carrying capacity. Figure 4A,B illustrates this relationship when aggregating biomass across all community compositions. To capture finer-scale variation, we also estimated species sensitivity within each specific community composition (Fig. 4C), highlighting how biotic interactions modulate species sensitivity.

Our analytical prediction of species sensitivity (Eq. 5) depends on species' SL, but also on the arithmetic and harmonic means of press intensities on species (κ_i). We estimated the press intensity as

$$\kappa_i = \frac{\max_T K_i(T) - \min_T K_i(T)}{\langle K_i(T) \rangle_T}.$$

which gives us the relative change in species' carrying capacity induced from temperature change, across the gradient considered.

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Code and data availability

The code used to produce the figures is available on Zenodo at [60]. The original data analyzed in this study is available on Zenodo at [61].

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