`estar`: An R package to measure ecological stability

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Abstract

1. Assessing ecological stability across populations or communities is a prime goal in biodiversity monitoring and conservation research. Quantifying stability is not trivial because its different aspects can be measured with various metrics. However, to date, no software enables measuring different stability metrics on ecological time-series data.

2. We present the `estar` R package that standardises and facilitates the use of ten established stability properties that have been used to assess systems' responses to press or pulse disturbances at different ecological levels (e.g. population and community).

3. `estar` provides two sets of functions. The first set corresponds to functions that can be applied to univariate data, i.e., a time series of a system's state variable (e.g., individual body mass, population abundance, or species richness). The metrics included in this set are: invariability, resistance, extent and rate of recovery, and persistence. The second set of functions can be applied to multivariate data represented by the time series of the abundances of all species in a community. The functions in this set measure the stability of a community at short and long time scales. In the short term, community's response to a pulse (sudden) perturbation is measured by maximal amplification, reactivity and initial resilience (i.e. initial rate of return to equilibrium). In the long term, stability can be measured as asymptotic resilience and intrinsic stochastic invariability.

4. The package includes vignettes demonstrating the use of all functions and an introduction to the multivariate autoregressive state-space models necessary for the second set of functions. `estar` constitutes a toolbox with standardised, ready-to-use functions that bridge dichotomies in definitions and enable comparisons across state variables, taxa and scales.

Introduction

Measuring stability at different levels of ecological organisation, from individuals to populations and communities, is of utmost importance for biodiversity monitoring and conservation because of widespread human-driven perturbations such as climate change, pollution, species invasions, and their multiple effects on biodiversity. Consensus emerges that ecological stability can be broadly defined as the 'overall ability of a system (…) to retain its function and structure in the face of perturbations' (Noy-Meir, 1973 *apud* Van Meerbeek et al., 2021)*,* but since its introduction in Ecology in the 1950s, stability has been shown to be a multidimensional concept (Donohue et al., 2013; Grimm & Wissel, 1997; Pimm, 1984; Van Meerbeek et al., 2021). This multidimensional character of stability manifests itself in at least four ways. First, different stability properties are not easily comparable because they are uncorrelated and capture different aspects of the system's response trajectory at different temporal scales (Donohue et al., 2016; Kéfi et al., 2019). Secondly, the same stability property can be measured at different organisational levels (Hillebrand & Kunze, 2020) or for different → *state variables* (e.g. total community biomass or Shannon index). Thirdly, different metrics have been proposed to calculate a single stability property. For example, resistance is often measured immediately after a perturbation but can also be measured when the difference between the state variable of the disturbed system and its pre-disturbed state is the largest (also known as "maximum attenuation", Capdevila et al., 2020). Further, different stability properties are not necessarily correlated (Arnoldi et al., 2018; Domínguez-García et al., 2019; Downing et al., 2020; Neubert & Caswell, 1997; Radchuk et al., 2019), making it necessary to estimate several of them when studying a system's stability. These four issues hamper synthesis across ecological stability studies. Beyond the necessity of quantifying multiple properties of stability, there is one practical concern: no software permits quantifying stability in the diverse ways it has been measured so far. Therefore, the time is ripe for a tool to measure different stability properties (or dimensions) in a standardised, comparable and reproducible way.

In addition to the multifaceted nature of the stability concept, there is a large divide between the metrics used by empiricists and theoreticians (Donohue et al., 2016). While empirical studies often measure the temporal invariability of population and community state variables, theoretical studies mainly quantify asymptotic stability properties derived from species interaction matrices (→ *species interaction matrix,* Donohue et al., 2016), which are rarely available for observational studies. Assessing interaction strength in empirical systems is a rather laborious task and can be accomplished with various methods (e.g. controlled pairwise species experiments; Carrara et al., 2015). However, estimations from different methods are usually not comparable (Carrara et al., 2015b). In that context, the first-order Multivariate Autoregressive Models (MARs) are a flexible method, as they can be applied to time-series data on community composition to derive species interaction matrices, which can be used to derive asymptotic stability properties (Downing et al., 2020; Ives et al., 2003). Still, the use of MARs outside of freshwater plankton community studies remains limited (Hampton et al. 2013). Therefore, a user-friendly tool that integrates MARs and allows the user to derive asymptotic stability properties has the potential to close the gap between empirical and theoretical stability research.

Here, we present `estar`, an R package designed to facilitate the use of ten stability properties. We present the properties in two groups, distinguished by the format of the input data: i) if the input is in the form of a time series of a single state variable measured at any organisational level we talk about **univariate properties** (invariability, resistance, extent of recovery, rate of recovery, and persistence; Table 1), and ii) if the input is a matrix of species abundances over time or a species interaction matrix, i.e. multivariate data, we talk about **multivariate properties** (maximal amplification, initial resilience, asymptotic resilience, intrinsic stochastic invariability, and intrinsic deterministic invariability; Table 2). We showcase the use of the package to measure the stability of a real-world freshwater invertebrate community perturbed by an insecticide (van den Brink et al., 1996).

Package overview

Although ecological stability attracts much research interest, we still lack R and Python software to readily calculate the variety of stability metrics available in the literature. At the community level, the *codyn* package (Hallett et al., 2020) provides four functions to measure stability in terms of species variances and covariance. The package MAR1 (Scheef & Holmes, 2023) offered functionality to both fit MARs and derive asymptotic stability properties from the output of those models, but it was taken down from R's centralized repository (CRAN) in 2019. The package MARSS, which can be used to estimate → *species interaction matrices*, does not provide formulas to calculate the stability properties (*sensu* Ives et al., 2003). Moreover, while MARSS has been used in aquatic communities (Hampton et al., 2013; Ruhí et al., 2015; Tolimieri et al., 2017), it remains largely unused in terrestrial systems. At the population level, the R package *popdemo* (Stott et al., 2021) allows performing transient analyses and thus calculating demographic resilience, a concept that was recently introduced to population ecology from community ecology (Capdevila et al., 2020). Further, although many stability properties (e.g. resistance and recovery rate) apply to a single time series (univariate data) and seem conceptually simple, no single software allows the quantification of all of them simultaneously. Thus, a tool is needed to derive asymptotic stability properties at the community level and stability properties from univariate time-series data (applicable to any level of organization). To address this, we provide the `estar` package. It has been submitted to CRAN and can currently be downloaded from https://anonymous.4open.science/r/estar-251E and installed from source: devtools::install.packages("estar", repos = NULL, type = "source").

Univariate stability properties

Univariate stability properties are calculated from the time series of a state variable measured in a system disturbed by a pulse disturbance (or white noise, in the case of invariability; Fig. 1-2, Table 1). These univariate properties can be calculated using a variable measured at any organisation level, for example, individual stress hormone levels, species richness, and Shannon-Weaver index. → *Baseline* is a central concept for quantifying multiple stability properties. The stability values depend on whether the state variable of the disturbed system is normalised relative to the baseline (Ingrisch & Bahn, 2018). Our functions give the user flexibility to specify the baseline and whether the state variable should be normalised by the baseline (e.g. by using the log ratio between the values measured on the disturbed and undisturbed systems).

We implemented functions to calculate five univariate stability properties. *Invariability* (*I*, `invariability()`, Fig. 2a), the most common stability measure (Donohue et al., 2016), measures the system's response to white noise. *Resistance* (*R*, `resistance()`, Fig. 2b) is the magnitude of change in the state variable following a disturbance (Pimm, 1984). It can be calculated as the maximum magnitude of change in the state variable or the magnitude at a user-defined time step after the disturbance (e.g. at the first time step to capture the system's initial resistance). *Recovery* is the return of the system's state variable to the baseline state (Medeiros et al., 2021; Van Meerbeek et al., 2021). `estar` contains two properties for it: the *extent of recovery,* i.e. how close the system returns to the baseline (*Er*, `recovery_extent()`, Fig. 2c) and the *rate of recovery*, i.e. how fast it returns to the baseline (*Rr*, `recovery_rate()`, Fig. 2d). Finally, *persistence* (*P*, `persistence()`, Fig. 2e) is the proportion of time a variable stays within one standard deviation from the baseline's mean during the user-defined period (Pimm, 1984). Descriptions of the variants of each metric and an evaluation of the functions' performance can be found in the vignette "Univariate metrics".

Multivariate stability properties

The multivariate properties measure the community's responses to a perturbation, both in the short-term and in the long-term. The long-term (asymptotic) rates are usually estimated for theoretical systems (Arnoldi et al., 2018; Neubert & Caswell, 1997), while empirical studies mainly assess the short-term (transient) rates (Arnoldi et al., 2018). The long-term data are rarely available for empirical systems, limiting the possibility of deriving dominant eigenvalues from → *Jacobian matrices* to calculate the asymptotic resilience of theoretical systems (Table 2).

In contrast to the single time series of the state variable that is required as data input for univariate stability properties, multivariate properties are calculated from species interaction matrices (denoted as → **B**). Our package requires the estimation of **B** from the user-supplied time series data on species abundances in the community (termed "multivariate data"). We provide the function (`extractB()`) to format the output of the multivariate autoregressive state space (MARSS) model fitted by the R package MARSS (Holmes et al., 2012; Holmes, Scheuerell, et al., 2024; Holmes, Ward, et al., 2024). MARSS models estimate **B** while accounting for uncertainty in the observation process that generated the data. We exemplify how MARSS models work and comment on possible pitfalls and the functions' performance in the "MARSS in *estar*" vignette.

We provide three functions to characterise a community's transient response to a pulse disturbance (Fig. 3). Two of these functions calculate the metrics describing the "amplification envelope" — the curve describing the upper bound response to a perturbation (Neubert & Caswell, 1997). The amplification envelope can be interpreted as an estimation of initial instability (Arnoldi et al., 2016) and is characterised by measures of *reactivity* (R_a, `reactivity()`, Table 2) and *maximal amplification* (A_{max}, `max_amp()`). Complementing the amplification envelope, the *initial resilience* (R_0, `init_resil()`) characterises the system's initial rate of return to equilibrium (Table 2, Arnoldi et al., 2018).

To measure stability in the long term, we provide a function to calculate *asymptotic resilience* (R_∞, `asympt_resil()`, Table 2, Fig. 3]), the long-term rate of return to equilibrium, complementary to R_0 (Arnoldi et al., 2018). Further, to measure instability under press disturbance or white noise, `estar` provides the *intrinsic stochastic invariability* (I_∞, `stoch_var()`), a theoretical equivalent of the univariate measure of invariability (Arnoldi et al., 2016), albeit uncorrelated to it (Downing et al., 2020).

Example: Stability of an aquatic macroinvertebrate community

To exemplify the use of `estar`, we applied it to data from a species-rich community of freshwater macroinvertebrates that was disturbed by the insecticide chlorpyrifos in a previously conducted eco-toxicological experiment (van den Brink et al., 1996). We analysed the effect of two concentrations of the insecticide on the abundance of three functional groups of aquatic macroinvertebrates (herbivores, carnivores, and detritivores; Supplementary information S3). According to the univariate properties, detritivores recovered better than carnivores and herbivores under the lower insecticide concentration, as quantified by the extent of recovery and rate of recovery (at week 28, Fig. 4-a, b). Under the higher insecticide concentration, carnivores had the highest rate of recovery because by week 28 their abundance increased to higher values in relation to their pre-disturbance state, whereas detritivores stayed at lower abundances. Finally, resistance (calculated as the magnitude of abundance change in the first week) was particularly low for the detritivores, demonstrating that resistance and recovery correlate negatively in this system.

Regarding the multivariate stability properties, the higher reactivity and maximal amplification values at high insecticide concentration reflect the strong decreases in herbivore and detritivore abundances (Table 3). Similarly, both the initial and asymptotic resilience were lower at a higher concentration of chlorpyrifos, indicating a slower rate of return to equilibrium compared to the communities subjected to a lower concentration. Nonetheless, we obtained much higher stochastic invariability for the community under higher insecticide concentration.

Conclusion

The `estar` package provides functions for calculating different stability properties, grouped in two sets: those applicable to time series 1) of single state variables and 2) of community compositional data. With the functions applied to time series of single state variables, we offer a flexible tool that quantifies stability at different levels of organisation, from individual to community. With the functions applied to community compositional data, we offer a tool for easy computing of the stability properties that were hitherto mainly used by theoreticians. Thus, `estar` closes the gap between empiricists and theoreticians in stability research. Finally, this package will facilitate cross-system comparisons of stability and further our understanding of how stable systems are across organisation levels, spatiotemporal scales and environmental conditions.

Glossary

Baseline: → *state variable* value(s) the user defines to represent an undisturbed system. It can be measured before a disturbance affects the focal system, from a separate undisturbed system, or from a single point considered to be representative of an undisturbed system (Fig. Error: Reference source not found-b).

Jacobian matrix: a functional matrix or derivative matrix of a differentiable function of all first partial derivatives in the case of total differentiability. The Jacobian is used, for example, to approximate multidimensional functions in mathematics or, in the community ecology context, for functions of interaction strength. → *Species interaction matrix.*

Press disturbances: a press disturbance affects a system permanently and continuously (Ryo et al., 2019), e.g. climate change or ongoing pollution from leakage.

Pulse disturbance: an event that suddenly affects a system and recedes quickly after reaching a peak, e.g. fires or storms (Ryo et al., 2019).

Species interaction matrix (**B**): a matrix quantifying the strength of density dependence between the n species in a community, i.e. the effect of one species' density on the per capita growth rate of another (or of its own, Hampton et al., 2013). It is often referred to as "community matrix" (or "a discrete-time version of a → *Jacobian matrix*"; Downing et al., 2020).

State variable: a variable describing a system, e.g. population abundance (whereby the population is a system) or species richness (whereby the community is a system).

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Table 1: Definitions of the univariate stability metrics and their variants, along with the options of baseline (b) used, and the options of response from which the metric is calculated. v_b refers to an independent baseline; v_p, to a baseline defined by pre-disturbance values; and v_d, to the state variable values in the disturbed time series; t stands for time. Notes: [a] usually the first time step following disturbance, [b] summarised as the mean or median of values of a user-defined time period, [c] usually the last time step of the time series, [d] time steps of disturbed systems and baseline match. User-defined values do not have a default value in the function.

Metric, function name	Formal definition (several definitions are possible for the same metric)	Baseline	Response	Notation of metric
Invariability (I, `invariability()`, also referred to as "temporal stability", Hillebrand et al., 2018)	The inverse of the standard deviation of residuals of the linear model where the response is predicted by time.	v_b, v_P	Log-ratio $l = log(v_d/v_b)$	$\frac{1}{\sigma(\varepsilon)}$, where $\sigma(\varepsilon)$ is the standard deviation of e, the residuals of the linear model $l = \beta t + \varepsilon$, with t referring to the time, β to the regression coefficients of the model, and ε to its errors.
		none	v_d	Same as above, but the response in the linear model is the state variable, $v_d = \beta + \varepsilon$
	The inverse of the coefficient of variation of response.	v_b	Log-ratio, l	$\frac{1}{CV(l)}$
		none	v_d	$\frac{1}{CV(v_d)}$
Resistance (R, `resistance()`)	Log response ratio between the state variable's value in the disturbed and in the baseline systems, on the user-defined time step[a].	v_b	Log-ratio	$\log(v_d/v_b)$
		v_p[b]	Log-ratio	$\log(v_d/v_p)$
	Maximal log response ratio between the state variable's value	v_b	Log-ratio	$\max(\log(v_d/v_b))$

	in the disturbed and the baseline systems, over user-defined time interval.	v_p	Log-ratio	$\max(\log(v_d/v_p))$
	Absolute difference between the state variable's value in the disturbed and in the baseline systems, on the user-defined time step[a].	v_b	Difference	$\lvert v_d - v_b \rvert$
		v_p	Difference	$\lvert v_d - v_p \rvert$
	Maximal difference between state variable's value in the disturbed and in the baseline systems, over user-defined time interval.	v_b	Difference	$\max(\lvert v_d - v_b \rvert)$
		v_p	Difference	$\max(\lvert v_d - v_p \rvert)$
Extent of recovery (E_r, `recovery_extent()`)	Log-response ratio between the state variable in the disturbed system and the baseline taken on the user-defined time step t_{post} when the recovery is assumed to have taken place[c].	v_b	Log-ratio	$\log(v_d/v_b)$
		v_p	Log-ratio	$\log(v_d/v_p)$
	Difference between the state variable in the disturbed system and the baseline, taken on the user-defined time step t_{post} when the recovery is assumed to have taken place[c].	v_b	Difference	$v_d - v_b$
		v_p	Difference	$v_d - v_p$
Rate of recovery (R_r, `recovery_rate()` - also called "engineering resilience" by Pimm (1984))	The slope of a linear model, where the response is predicted by time.	v_b	Log-ratio, l	$l = R_r.t + b$
		none	v_d	$v_d = R_r.t + b$

Persistence (P, `persistence()`)	The proportion of the user-defined time frame t_a during which the response stayed within the limits of an interval determined by the baseline mean ± sd (t_P).	v_b	v_d	t_P/t_a

Table 2: Definitions of the multivariate stability metrics, based on species interactions matrix (**B**).

Metric, function name	**Formal definition and interpretation**	**Equation**
Reactivity (R_a, `reactivity()`)	Maximum initial amplification rate of a perturbation (Neubert & Caswell, 1997).	$\lambda_{dom}(H(B))$, where λ_{dom} is the dominant eigenvalue, and H is the Rayleigh quotient.
Maximal amplification (A_{max}, `max_amp()`)	The factor by which the perturbation that grows the largest is amplified, calculated as the Euclidian norm of the species interaction matrix (Neubert & Caswell, 1997).	$A_{max} = max_{t\geq 0}(max_{x_0 \neq 0} \frac{\lVert e^{B^T} x_0 \rVert}{\lVert x_0 \rVert})$, where $|e^{B^T} \vee$ is the matrix norm of **B** and x_0 is the vector of initial abundances (Domínguez-García et al., 2019).
Initial resilience (R_0, `init_resil()`)	Initial resilience is calculated as the initial rate of return to equilibrium (Downing et al., 2020). The larger its value, the more stable the system, as its "worst case" initial rate of return to equilibrium is faster (Downing et al., 2020).	$R_0 = -log\left(\sqrt{\lambda_{dom}(B^T B)}\right)$
Asymptotic resilience (R_∞, `asymp_resil()`)	The slowest/long-term asymptotic rate of return to equilibrium after a pulse perturbation (Arnoldi et al., 2016; Downing et al., 2020). R_∞ is a positive real number. The larger its value, the more stable the system, as its rate of return to equilibrium is faster (Downing et al., 2020).	$R_\infty = -log(\lvert\lambda_{dom}(B)\rvert)$

Intrinsic stochastic invariability (I_S, `stoch_var()`)	Inverse of the maximal response variance to white noise. The larger its value, the more stable the system, as its rate of return to equilibrium is higher.	$I_S = \frac{1}{\|\hat{B}^{-1}\|}$where $\|\hat{B}^{-1}\|$ where the spectral norm of the inverse of matrix $\|\hat{B}^{-1}\| = B \otimes I + I \otimes B$, with I being an identity matrix.

Table 3: Multivariate metrics calculated by `estar` for the aquatic macroinvertebrate community subjected to two concentrations of the chlorpyrifos insecticide.

	Insecticide concentration	
	0.9 µg/L	6 µg/L
Multivariate metrics		
Reactivity	0.593	0.972
Maximal amplification	2.308	3.14
Stochastic invariability	7.510	119.061
Initial resilience	0.350	0.275
Asymptotic resilience	0.651	0.173

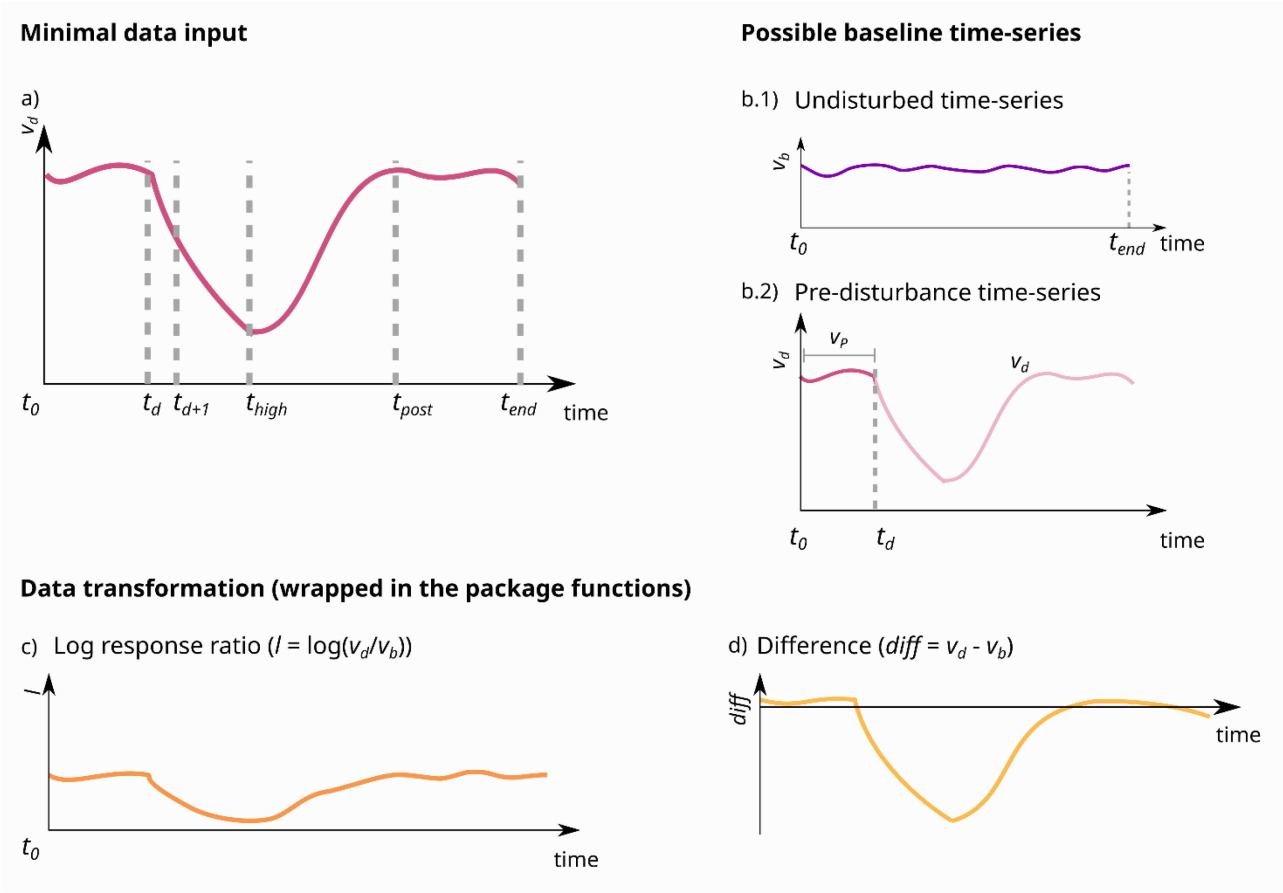

Figure 1: Schematic representation of possible univariate inputs (a and b) and the two types of transformation applied for some metrics (c and d). Relevant time steps: t_d time when pulse disturbance is applied to the system, t_{d+1} first time step after disturbance, t_{high} time step where the absolute distance between state variable value in the disturbed system and baseline is the highest, t_{post} time step where recovery is considered to have happened, t_{end} end of time series. a) The data for which a metric is to be calculated must constitute a time series of a state variable in the disturbed system (v_d). b) Most functions require a time series of the same state variable in the baseline system. This baseline can be taken from a separate undisturbed system (v_b, b.1) or from the pre-disturbance values of the disturbed system (v_p, b.2). It can be a single value or a summary of the time series. The stability metrics that require both the disturbed and baseline time series are applied to either the log response ratio (l) between the values in these two time series (c) or the difference between them (d).

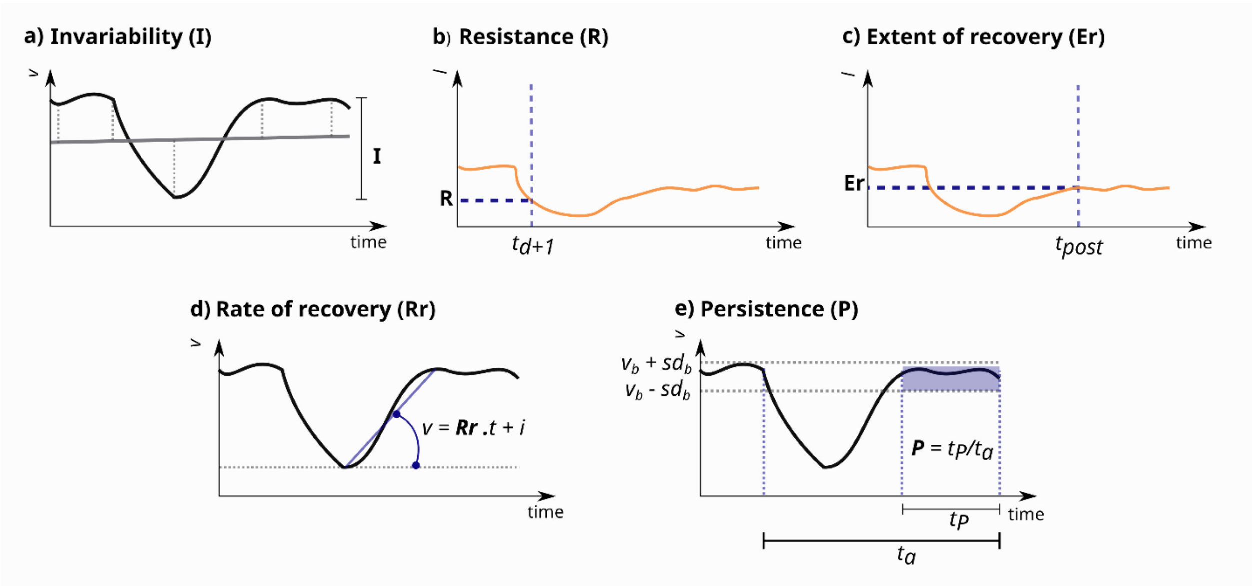

Figure 2: Schematic representation of how some of the variants of univariate properties are calculated with estar: a) invariability (*I*) as the coefficient of variation of the state variable in the disturbed state; b) resistance (*R*) as the log-ratio (*l*) between the disturbed and baseline time series in the first time step after disturbance (t_{d+1}); c) extent of recovery (*Er*) as log-ratio between the disturbed and baseline time series at the user-defined time step the system is expected to have recovered (t_{post}); d) rate of recovery (*Rr*) as the slope of the linear model fitted to the disturbed time series; and e) persistence (*P*) calculated as the proportion of time during which the disturbed time series stayed in the interval defined as +/- 1 standard deviation from the baseline ($v_b \pm sd_b$) over the total user-specified time period (t_a). The metrics are calculated from a time series of a state variable (*v*; black line) and the log response ratio (*l*; orange line). All variants are demonstrated in the "Univariate properties" vignette.

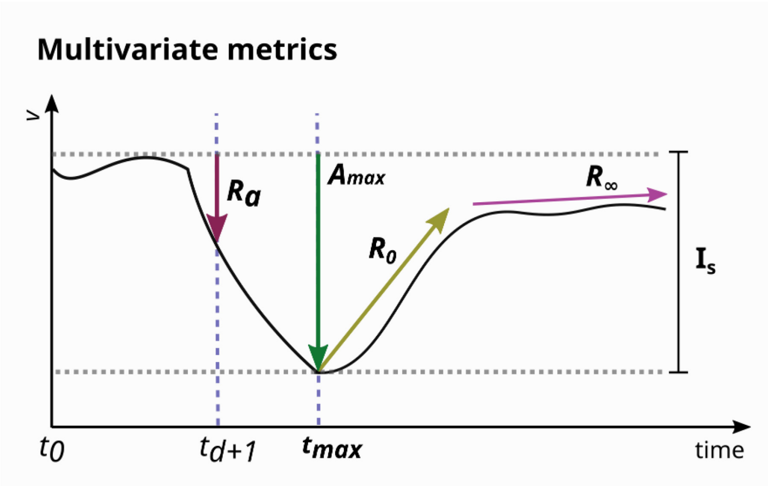

Figure 3: Schematic representation of the multivariate properties: reactivity (R_a), calculated at the first time step following disturbance (t_{d+1}); maximal amplification (A_{max}); initial resilience (R_0); asymptotic resilience (R_∞); and intrinsic stochastic invariability (I_S). To facilitate comprehension, we illustrate metrics in relation to a state variable (*v*) disturbed at time t_d, but the metrics, in fact, are calculated from the community's species interactions matrix and not a single state variable. All properties are demonstrated in the "MARSS models" vignette.

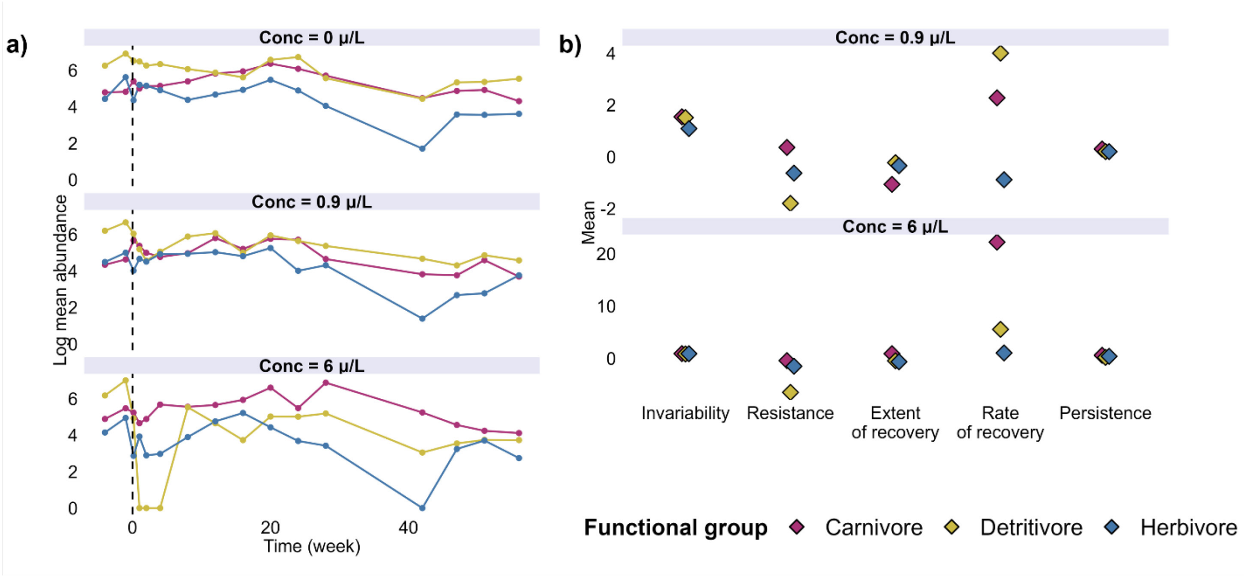

Figure 4: Example of estar application to measure the stability of three macroinvertebrate functional groups to two concentrations of the chlorpyrifos insecticide. a) Log of mean abundance over the 60 weeks of the experiment. Insecticide was applied at week 0 (vertical dashed line). b) Univariate metrics calculated by estar under two concentrations of the insecticide (0.9μg/L and 6μg/L).