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Software note

'mixglm': an R package for estimation of stable states, tipping points, and ecosystem resilience using mixture models

Adam Klimeš[1,2], Joseph Daniel Chipperfield[3], Joachim Paul Töpper[3], Marc Macias-Fauria[4], Marcus Spiegel[5], Vigdis Vandvik[1], Liv Guri Velle[6,7], Alistair William Robin Seddon[1]

[1]Department of Biological Sciences, Faculty of Mathematics and Natural Sciences, University of Bergen, Bjerknes Centre for Climate Research, Bergen, Norway
[2]Department of Geoecology, Institute of Botany of the Czech Academy of Sciences, Třeboň, Czech Republic
[3]Norwegian Institute for Nature Research, Bergen, Norway
[4]Scott Polar Research Institute, University of Cambridge, Cambridge, UK
[5]Biogeosciences Lab, School of Geography and the Environment, University of Oxford, Oxford, UK
[6]Møreforsking, Ålesund, Norway
[7]Norwegian Institute of Bioeconomy Research, Trondheim, Norway

Correspondence: Adam Klimeš (adamklimes3@gmail.com)

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A number of modelling frameworks exist to estimate resilience from ecological datasets. A subset of these frameworks seeks to estimate the whole 'stability landscape', which can be used to calculate resilience and identify stable states and tipping points. These methods provide opportunities for insights into possible causes and consequences of variation in ecosystem resilience and dynamics. However, because such models can be complex to implement, there has so far been a substantial barrier to their application in ecological research. Here, we present the 'mixglm' package for R software, which parametrizes stability landscapes using a mixture model approach. It provides tools for the calculation of resilience, identification of stable states and tipping points, as well as visualization functions. Flexible model specification allows the mean, precision, and probability of each mixture component to be linked to multiple predictors, such as environmental covariates. 'mixglm' is based on Bayesian inference via NIMBLE and supports normal, beta, gamma, and negative binomial distributed response variables. We illustrate the use of 'mixglm' with a published case of tree cover in South America, which reports a stability landscape with distinct stable states. Using 'mixglm', we replicated the identification of these states. Moreover, we quantified the uncertainty of our estimates, and computed resilience estimates of South America's forests. We also conducted a power analysis to provide guidance regarding required sample sizes. 'mixglm' can be readily used to describe stability landscapes and identify stable states in most spatial datasets, and it is accompanied by tools for the calculation of resilience estimates.

Keywords: critical transitions, mixture model, resilience, stability landscape, stable states, tipping points

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Introduction

Under certain conditions, ecological systems may exist as alternative stable states separated by thresholds or tipping points (Scheffer et al. 2001, Pausas and Bond 2020). Transitions between these states can result in large differences in ecological structure and functioning, such as those between forested and non-forested systems. Because transitions between alternative states can occur abruptly and be difficult to reverse, there is global concern about the status of multiple Earth system components and their potential for abrupt change, both at local and global scales (Armstrong McKay et al. 2022). To avoid or adapt to these changes, information about stable states of systems, their alternative equilibria, the associated ecological thresholds, and, more generally, variation in ecosystem resilience across space and time are of primary importance.

Resilience and related concepts can be illustrated using a stability curve with valleys representing stable states and hilltops representing tipping points (Fig. 1A; Hodgson et al. 2015, van Nes et al. 2016). In this analogy, the system state is shown as a ball rolling along this curve, and its resilience is defined either as the system's response to small perturbations of the given state variable (known as engineering resilience) or to larger perturbations that risk the system crossing a tipping point and shifting into a basin of an alternative stable state (ecological resilience; for a review of various resilience metrics, see Dakos and Kéfi (2022)). A change in the stability curve along an external (e.g. climatic) gradient then constitutes a stability landscape (Fig. 1B; sensu Scheffer et al. (2001)). The existence of one or more stable states generally varies along such gradients (Scheffer and Carpenter 2003).

While the ideas that underlie the presence and location of alternative stable states and resilience have long been recognized, practical applications to identify stable states and, more generally, estimate resilience in empirical datasets remain a challenge (Scheffer and Carpenter 2003). Such applications can be divided into two types: the first type uses time series data (or spatio-temporal data), and the second uses spatial datasets. Time series analyses have been used, for example, to identify abrupt changes in a given state variable (Smith et al. 2022); to identify changes in the statistical properties of a state variable over time, which may provide measures of resilience (Feng et al. 2021, Forzieri et al. 2022, Rocha 2022); to categorize trajectories of state variables (Sánchez-Pinillos et al. 2024); or to estimate the stability landscape using potential or quasi-potential (Livina et al. 2010, Nolting and Abbott 2016). A limitation of these approaches is the length of available time series, which, for many data sources, does not exceed a few decades (Bathiany et al. 2024).

While time series data of relevance for ecosystem resilience spanning extended temporal windows are rare, spatial datasets are more readily available. When the spatial dataset is continuous, properties of the spatial patterns of the system may be used to estimate resilience (similarly to time series analyses – e.g. autocorrelation; Génin et al. 2018). Alternatively, we can use the distribution density of a state variable in relation to external predictor(s) to describe the whole stability landscape (Hirota et al. 2011, Scheffer et al. 2012). Access to the whole stability landscape allows us not only to calculate several measures of resilience (Dakos and Kéfi 2022) but also to assess the number and properties of stable states and tipping points. Under this method, high probability density is interpreted as the presence of a stable state, while local minimum of probability density is interpreted as the presence of a tipping point. However, due to model complexity, this approach is rarely used or is not used to its full potential (e.g. using none or only one external predictor; Hirota et al. 2011).

Here, we present the R package 'mixglm', which, for a spatial dataset, can parametrize a stability landscape using a mixture model, identify stable states and tipping points, and calculate resilience (https://github.com/adamklimes/mixglm). We illustrate its use on tree cover in the tropical region of South America (recreating analyses done by Hirota et al.

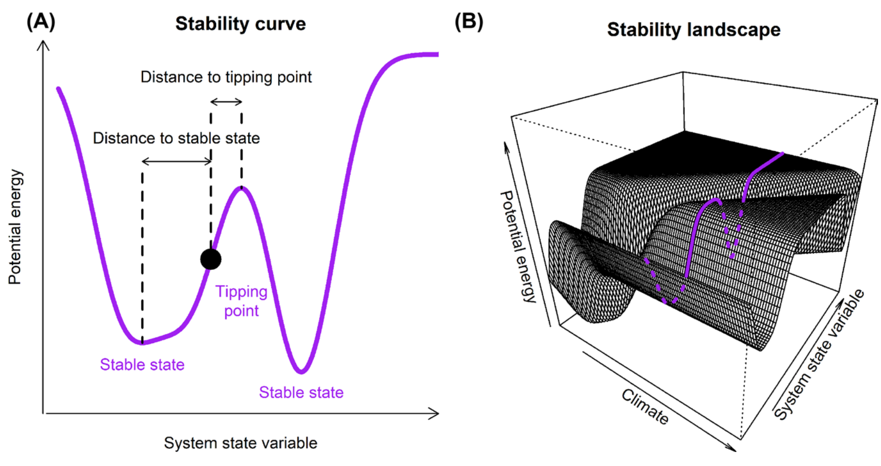

Figure 1. (A) Stability curve with two stable states. The black point denotes an instance of the system. (B) Stability landscape: the stability curve can change along an external gradient (here, climate) resulting in a stability landscape. Purple line highlights the stability curve from Fig. 1A.

(2011) and Flores et al. (2024)). We also run a power analysis to provide guidance regarding the required sample size.

Mixture model

A stability landscape can be approximated by a mixture model. Mixture models are probabilistic models where the probability density function is a sum of component densities (typically of one parametric family, such as Gaussian), each multiplied by its probability in the mixture (often called mixing proportions; McLachlan et al. 2019). Mixture models have been used for more than 100 years for purposes such as cluster analyses or modelling of data with complex distributions where a single probability distribution is not adequate (Pearson 1893). An extreme case, where the number of components equals the number of observations, is a nonparametric kernel density (previously used for estimation of stability landscapes; Hirota et al. 2011). Mixtures with component parameters depending on predictors (sometimes called mixtures of regressions; De Veaux 1989) thus represent a parametric (or semiparametric) solution for modelling stability landscapes.

In 'mixglm', each component in the mixture can have its mean, precision (the inverse of variance), and probability dependent on one or multiple external predictors (such as climate, land-use intensity, or site identity). Furthermore, these predictors can differ for mean, precision, and probability, but also among mixture components. This flexibility allows the approximation of complex stability landscapes where one or more stable states and their properties (e.g. width of basin) can change along multiple external (climatic) gradients.

In other words, a mixture model can be understood as several linear regressions combined. Each of these regressions can have multiple predictors (i.e. they are multiple regressions). Furthermore, these regressions do not need to have homogeneous precision (inverse of variance) – the precision can change along these (or any other) predictors. Finally, these regressions are combined, but their weights do not have to be identical. Some regressions can be more strongly represented in the overall mixture than others (thus more strongly determining the overall probability density). These weights can also change along predictors, meaning that the regressions that are dominant in the mixture can vary along, for example, a climatic gradient.

This mixture can be written (using matrix notation) as:

$$y = \sum_{i=1}^{n} \frac{\log\left(\phi_i X\right)}{\sum_{i=1}^{n} \log\left(\phi_i X\right)} \times \left(\beta_i X + \frac{1}{\log\left(\gamma_i X\right)} \times \varepsilon\right)$$

where $\log(\phi_i X)$ is a weighting term (probability of a component in the mixture), which is divided by the sum of all weights to ensure that weights sum to 1, y is a system state variable (e.g. tree cover), β is a vector of parameters for mean, γ is a vector of parameters for precision, ϕ is a vector of parameters for the probability of components in the mixture, X is the matrix of predictors (with the possibility for different values of mean, precision, and probability for each component), log is the natural logarithm, ε is a normally distributed error term, and n is the number of components in the mixture. In addition to a mixture of normally distributed components, 'mixglm' also supports mixtures of beta (default link function: logit), gamma (link: log), and negative binomial (link: log) distributions. All distributions are parametrized using mean and precision (full list of implemented link functions: identity, log, logit, probit, and cloglog).

The number of components in the mixture model does not have to (and typically does not) correspond to the number of stable states of the system. This is because stable states of the system are not mean values of underlying components but rather modes of the overall mixture (compound distribution). A mixture of multiple components can thus describe one stable state with a wide basin. Therefore, the number of components used in the mixture ought to be higher than the expected number of stable states of the system. Components that do not increase the data likelihood will have a probability close to zero and will thus be effectively suppressed. The number of components for a particular dataset can be determined using the Watanabe–Akaike information criterion (WAIC; Watanabe 2013).

The fitted model is then used to infer stable states, computed as local maxima in the compound distribution (stability landscape), and tipping points, computed as local minima of the compound distribution. With these, various measures describing the position of observations in the stability landscape or their ecological resilience can be determined – these include probability density, distance to the closest stable state or tipping point (precariousness), and potential depth (difference in probability density in relation to the closest tipping point; for a detailed description of resilience measures see Dakos and Kéfi (2022)).

The combination of probability densities of several mixture components can lead to multiple local minima and maxima in the stability landscape. Some of these may only represent small 'bumps' in the stability landscape, which are unlikely to be real stable states or tipping points, and which have large uncertainty regarding their existence and/or position in the landscape. For calculation of some derived characteristics, such as distance to the closest stable state or tipping point, it is preferable to avoid these local minima and maxima. To do so, 'mixglm' scales the probability density for each stability curve to range from 0 to 1. To avoid misclassification of stable states/tipping points, the package provides an option to only consider those local minima and maxima that differ in their scaled density by a specified threshold.

The mixture model is implemented in the 'mixglm' R package (www.r-project.org), internally using NIMBLE (de Valpine et al. 2017) to fit the model within a Bayesian framework. We use the Bayesian framework because it enables the above-described flexibility of the model, provides uncertainty in results (below), and the user can specify priors for all parameters, which allows incorporation of prior knowledge of the system into the inference.

In addition to 'mixglm', other packages to fit mixture models exist in R, which could be useful for model comparison, alternative parametrizations, or for mixtures of specific distributions. Mixtures are typically fitted using variants of the EM algorithm (Dempster et al. 1977), which can handle predictors for mean (De Veaux 1989), but most current implementations assume constant variance of each component and, more importantly, constant probabilities of components within the mixture (which is rarely suitable for estimation of stability landscapes). Package 'mixtools' (Benaglia et al. 2009) can be used for mixtures of regressions, which are normally Bernoulli or Poisson distributed (but only the first option allows the probability of components to vary along predictors). Package 'flexmix' (Grün and Leisch 2008) can be used for mixtures of generalized linear models, and it has an option for estimation of the probability of components in the mixture to be implemented using so-called concomitant variable models (Grün and Leisch 2008). Within the Bayesian framework, there are packages to estimate mixtures of distributions but without any predictors (e.g. 'bmixture' (Mohammadi 2022) or 'bayesmix' (Grün 2023); for a method overview, see Mengersen et al. (2011)).

Case study

To illustrate the use of the 'mixglm' package, we selected a published example of a system with multiple stable states – tree cover in South America along a precipitation gradient, which was described as having alternative stable states: forest and savanna (and potentially a treeless state, but that cannot be reliably demonstrated using the tree cover dataset; Hirota et al. 2011, Hanan et al. 2014, Flores et al. 2024). We modelled the tree cover for 4860 randomly selected locations using a mixture of seven beta-distributed components (to ensure a higher number of components than stable states), with precipitation as a predictor for mean, precision, and probability of all mixture components (for details, including use of multiple predictors, see the Supporting information and vignette article: https://adamklimes.github.io/mixglm/).

Using 'mixglm', we were able to reconstruct the stability landscape for tree cover along the precipitation gradient in South America using an updated dataset and to identify forest and savanna as alternative stable states (Fig. 2A), including the associated uncertainty of their presence (see the Supporting information). 'mixglm' provides tools for further exploration of results and calculation of various metrics of interest. Underlying mixture components can be visualized using the *plot()* function, and the *sliceMixglm()* function enables plotting of stability curves for individual precipitation values (see the Supporting information). The stability landscape can be used to determine the domain to which each observation falls and map its alternatives (Fig. 2B, C), thus providing risk areas regarding potential transitions to alternative stable states. Furthermore, these can be accompanied by quantitative measures describing the conditions of specific observations and their ecological resilience (Fig. 2D), such as 'potential depth' (Dakos and Kéfi 2022), a measure that estimates how easily a given system can be 'pushed' into an alternative stable state. Finally, the model can be easily used for predictions of future stability landscapes, including their stable states (Fig. 2E), tipping points, and resilience measures (for further details about the case study, see the Supporting information).

Power analysis

To assess the power of the mixture model and to provide guidance on the required sample size for the estimation of stability landscapes and identification of stable states in a system, we performed several power analyses. We generated data by first assigning each observation randomly to one of two states (each with 50% probability), generated predictor values from a uniform distribution ranging from 0 to 1, and generated a system state variable from a normal distribution with the mean depending on the assigned state and SD of 1. We changed sample size, distance between the states, and shift – the overlap of those states along the predictor – by increasing predictor values for one of the states:

$$\text{State} \sim \text{Bernoulli}\left(0.5\right)$$

$$\text{System State Variable} \sim \text{Normal}\left(\text{State} \times \text{Distance, SD} = 1\right)$$

$$\text{Predictor} \sim \text{Uniform}\begin{pmatrix} \text{from} = 0 + \text{Shift} \times \text{State,} \\ \text{to} = 1 + \text{Shift} \times \text{State} \end{pmatrix}$$

where Distance and Shift are pre-specified scalar values. For each combination of parameters, we ran 100 models and assessed power as the proportion of models in which an alternative stable state was identified for all observations (in case of Shift > 0 only for observations with overlapping predictor values).

Power analysis showed that a sample size of at least 200 was necessary when using this mixture model for reliable identification of alternative stable states. To be identifiable as distinct (with sample size 200), distances between stable states had to be at least 4 standard deviations from each other, and the stable states could overlap only slightly along the predictor gradient at the expense of a slight decrease in power (Supporting information).

Discussion

We have shown that the 'mixglm' package effectively manages to estimate the stability landscape including quantification of uncertainty (Supporting information), identifies stable states and tipping points, and provides measures of ecological resilience in a system described by a spatial dataset. 'mixglm' employs a mixture of regressions rather than only a mixture of distributions (without predictors) as previously used for

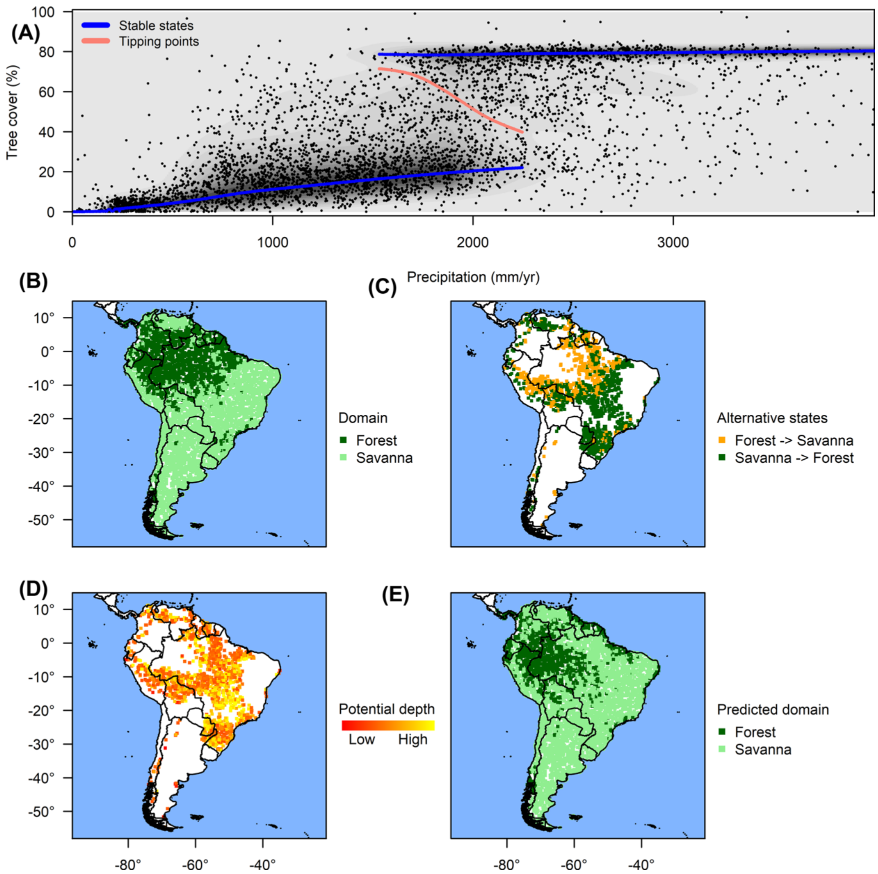

Figure 2. Selected results from the case study on tree cover in South America. (A) Stable states in tree cover along a precipitation gradient. Blue lines denote putative stable states, and the red line denotes a tipping point. Shading corresponds to probability density (scaled). (B) Domains for each observation. A domain is defined as the stable state for each observation (basin in the stability landscape). (C) Alternative stable states. Part of the area (31.1% of forest and 29.7% of savanna) has an alternative stable state given the precipitation values. (D) Potential depth is one of several resilience measures available in 'mixglm'. This represents a difference in probability density between a given observation and its closest tipping point. Low potential depth (red color) denotes low resilience. (E) Predicted domain for the end of the 21st century. Prediction is based on precipitation from the CORDEX South America model, scenario RCP 4.5 (intermediate scenario) for the period 2081–2100 (Gutiérrez et al. 2021, Iturbide et al. 2021). Domain change is predicted for 37.5% of forest and 6.8% of savanna.

identification of stable states (Fig. 1 in Hirota et al. (2011) and Fig. 1 in Scheffer et al. (2012)). This allows us to relax the assumption that stable states have a constant value of the system state variable along a climatic gradient and thus are identifiable based on the overall distribution of the state variable. The stability of a system state refers to an equilibrium among its components: that is, it does not require the state variable to be constant (e.g. along a climatic gradient). As stable states are often maintained by the interaction of multiple drivers (such as herbivory, fire frequency, population dynamics; van Langevelde et al. 2003), and these drivers are likely climate-dependent (Staal et al. 2018), we can expect a system stable state value to change along, e.g. a climatic gradient. Therefore, the identification of stable states should take the climatic or other environmental gradient(s) into consideration, e.g. as predictor(s) in a mixture model.

The parametric solution for the estimation of the stability landscape and identification of stable states in 'mixglm' provides higher statistical power than the non-parametric solution using a kernel smoother (implemented in R package 'earlywarnings'; Dakos et al. 2012). This is especially true for very close alternative stable states (for power comparison, see the Supporting information). However, a non-parametric approach might still be preferable when a particular distribution of mixture components cannot be assumed. A parametric solution also enables the user to make inferences about ecological drivers of the system based on parameters of components in the mixture, although caution is necessary, as the estimation of mixtures can be challenging (Hurn et al. 2003), especially with different combinations of components approximating the same stability landscape. Since 'mixglm' allows for the constraining of the parameters of individual mixture components, it can be used to test hypotheses about ecological drivers of the system.

Generally, using spatial datasets to estimate stability landscapes requires a suitable ecosystem state variable. Since the distribution of this variable is used, there must be no discontinuities caused by its calculation. Therefore, variables which are calculated using categorical inputs, such as land cover types, might not be suitable. Even without such inputs, complex algorithms can lead to discontinuities or decreased resolution in parts of the distribution of the ecosystem state variable, which might limit the interpretation. This is also the case for tree cover (Hansen et al. 2003), which has been shown to not be suitable for small geographical scales and has poor resolution in low tree cover values (Hanan et al. 2014, 2015, Staver and Hansen 2015). The opposite problem could arise from smoothing techniques or interpolation, which could mask out multimodality in the ecosystem state variable. On the other hand, spatial datasets where these techniques (Li and Heap 2008) are used are typically large enough that the smoothing is likely to take place on much finer scales, and should therefore not affect overall multimodality. With very small datasets or narrow and closely positioned stable states, we would recommend using primary (not interpolated) data, or at least checking the effect of interpolation.

The 'mixglm' package offers tools for estimation of resilience and identification of stable states which can be used in various ecological settings where stable states and/or resilience are of interest, ranging from lakes and wetlands to heathlands and drylands (Davidson et al. 2023). By using a well-established and flexible regression framework, it holds high potential for further development, e.g. by including terms in the model describing spatial autocorrelation. To facilitate any further development, the package provides an option to specify the NIMBLE model without fitting it (see function *mixglmSpecification()*). The 'mixglm' package is available at https://github.com/adamklimes/mixglm.

To cite 'mixglm' or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for 'ver. 1.0':

Klimeš, A., Chipperfield, J. D., Töpper, J. P., Macias-Fauria, M., Spiegel, M., Vandvik, V., Velle, L. G. and Seddon, A. W. R. 2025. mixglm: an R package for estimation of stable states, tipping points, and ecosystem resilience using mixture models. – Ecography 2025: e08148 (ver. 1.0).

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Author contributions

Adam Klimeš: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Software (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Joseph Daniel Chipperfield**: Conceptualization (equal); Methodology (equal); Software (equal); Supervision (supporting); Writing – review and editing (supporting). **Joachim Paul Töpper**: Funding acquisition (equal); Project administration (equal); Supervision (supporting); Writing – review and editing (supporting). **Marc Macias-Fauria**: Conceptualization (equal); Writing – review and editing (supporting). **Marcus Spiegel**: Writing – review and editing (supporting). **Vigdis Vandvik**: Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **Liv Guri Velle**: Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **Alistair William Robin Seddon**: Conceptualization (equal); Supervision (lead); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Code for all analyses is available on GitHub: https://github.com/adamklimes/mixglm_paper; 'mixglm' package: https://github.com/adamklimes/mixglm. No new dataset was produced in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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