Chapter 11

Long Time-Scale Recurrences in Ecology: Detecting Relationships Between Climate Dynamics and Biodiversity Along a Latitudinal Gradient

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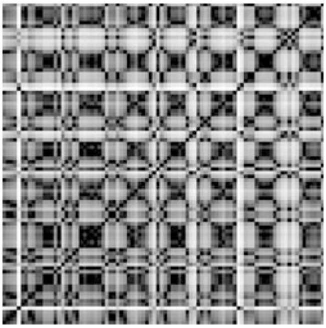

Abstract Climate is an important driver of ecological dynamics. However, many quantitative methods still ignore the fact that both ecological and climatic dynamics are inherently non-linear. While temporal variability is commonly measured as

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the standard deviation of the records in a time-series, temporal determinism and predictability can be measured using the approach of Recurrence Plots–Recurrence Quantification Analysis (RP–RQA). In this study, we explore the relationship between climate dynamics and biodiversity of two taxonomic groups (mammal species and tree family richness) over the North- and South-American landmasses. We found that higher biodiversity levels in both taxonomic groups are associated to lower values of climate predictability, determinism and variability in monthly temperature data. Our results also revealed a multiplicity of climate–biodiversity relationships, suggesting that the mechanisms underlying large-scale geographic variations in biodiversity may be more complex that originally envisioned.

11.1 Background

Ecology is the study of how organisms relate to one another and to their surroundings. Because organisms interact in many ways with both their biotic and abiotic environment, ecological dynamics may be highly non-linear and have inspired expressions such as: “on the edge of chaos” [1], “dynamically transient” [2], and “subject to critical transition” [3]. Yet, when confronted with such an array of dynamical behaviors, many ecologists do not know how or what to analyze in a time-series. In fact, most time-series in ecology are still characterized using mean and standard deviation measures, thus discarding information that may (or may not) be relevant to the understanding of ecological processes.

Climate is an important driver of ecological dynamics. Independently of biotic factors such as competition for resources, reproductive success, or predator–prey interactions, populations tend to be more abundant if climatic conditions are favorable to them and to decline if conditions are too harsh. Community ecology in particular has a long history of relating the global geographic distribution of species richness and diversity to contemporary climatic conditions [4]. Early successes of correlating taxonomic biodiversity to climatic variables, such as the long-term mean of annual temperature and precipitation, have bolstered the search for a mechanistic underpinning of these relationships (reviewed in [5]).

Other studies have emphasized that time-series of climatic variables can be described and interpreted in contrasting ways. Using long time-series of air temperatures at a spatial resolution of 0.5° over the globe, von Bloh et al. [6] showed that even though monthly temperatures at low latitudes do not fluctuate much, seasonal and inter-annual temperature dynamics are harder to forecast near the equator than towards the poles. In another study conducted in the Qinghai-Tibet plateau region, Zhao et al. [7] showed that the temporal determinism and predictability of temperature dynamics has decreased over recent decades, more prominently so in croplands and urbanized areas. The above studies have in common that they both used the method of recurrence plots to describe the determinism and predictability of time-series.

Recurrence plots are an excellent method for detecting dynamical patterns in time series [8], and, coupled with recurrence quantification analysis, permit the characterisation and detection of deterministic structures that may not be captured using classical statistical methods. Recurrence analysis should be of particular interest to ecologists as it is well-adapted to the analysis of short time series and, in its multivariate form, provides a valuable tool for detecting and describing nonlinear relationships between dynamical processes. In this chapter, we demonstrate the use of recurrence quantification analysis to explore the relationship between climate and biodiversity over large geographic scales.

11.2 Recurrence Plots and Recurrence Quantification Analysis

Recurrence plots (RP) were developed in statistical physics by Eckmann et al. [9] to visualize the system states in a phase space. System states are reconstructed by the method of time-delay embedding (see [8]). To illustrate how embedding works, let us create a time-series of plant species abundances surveyed over six consecutive years: 15, 25, 5, 7, 10, and 28 individuals per square meter. We define the dimension (the number of independent variables needed to capture a particular dynamic such as plant abundances e.g., $m = 3$) and time-delay (the time lag which minimizes autocorrelation, e.g., $d = 2$) of the embedding. Using these two parameters we reconstruct the system states from the above time-series, yielding the two successive states of: [15, 5, 10] and [25, 7, 28]. If n is the time-series length, one can only reconstruct $n - d(m - 1)$ system states. For example, embedding the above time-series with parameters of $m = 4$ and $d = 1$, three reconstructed states are obtained: [15, 25, 5, 7], [25, 5, 7, 10] and [5, 7, 10, 28]. The RP is then a square matrix, with time on both axes, of pairwise Euclidean distances between the reconstructed system states to which a distance threshold (*thresh*) is applied. A black dot in the plot indicates the presence of a “recurrence”; i.e., two system states that differ by less than the threshold (Fig. 11.1). If the threshold is too large, most states are considered similar and the plot is mainly black. Conversely, if the threshold is too small, most states are considered different and the plot is mainly white. RPs can be visually interpreted to detect non-stationary dynamics with either smooth or abrupt transitions, as well as identifying the presence of periodic and non-periodic processes (e.g., [10]). Several algorithms have been proposed to assist the analyst with the choice of m, d and *thresh* parameters [8].

Recurrence quantification analysis (RQA) forms a toolbox of mathematical measures for characterizing RPs [11]. In particular, RQA is capable of detecting the signature of chaotic dynamics in long time-series [12, 13]. In the ecological sciences, however, the time-series are usually too short or stochastic for detecting chaos or assessing the dimensionality of the system (i.e., the minimum number of variables required for capturing the system’s dynamics). Nevertheless, RQA allows

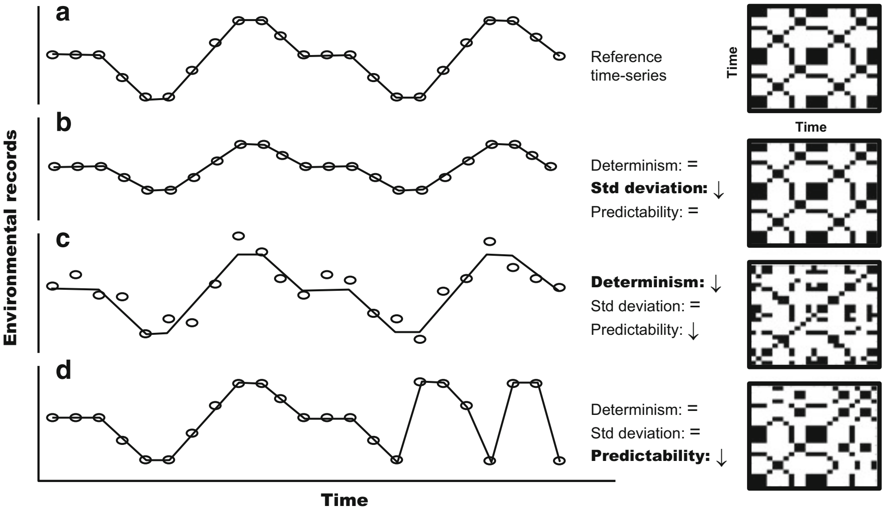

Fig. 11.1 Representation of a reference time-series of environmental (ecological or climatic) records (**a**) to which modifications were applied by: reducing variance (**b**), increasing stochasticity (**c**), introducing regime shifts (**d**). Next to the time-series are reported the effects of these modifications (↓ or =) on measures of temporal variability (std. deviation), determinism and predictability. Recurrence plots (with $m = 1$, $d = 1$, and 10 % recurrence rate) are displayed on the right-hand side

Table 11.1 Three fundamental measures of ecological and climatic dynamics

Measure	Definition	Measure	Comment
Temporal variability	Fluctuation of environmental records in a time-series	Standard deviation (*SD*) of the environmental records	Temporal variability depends on the scaling of the records and has no upper bound
Temporal determinism	Recurrence of two environmental states over time (see text)	Percentage of recurrences that are part of diagonal lines with 2 or more recurrences (*DET*)	Temporal determinism is a reciprocal measure of temporal stochasticity
Temporal predictability	Time period over which environmental states can be predicted into the future	The average length of diagonal lines in the RP (*length*)	Temporal predictability can be low even if determinism is high

us to calculate dynamical measures (Table 11.1) that are *a priori* unrelated to those of central tendency and variance and which may provide some indication of the degree of determinism in a system, even for short time series.

11.3 Ecological and Climatic Dynamics

Ecological and climatic dynamics can be characterized along three major axes (Table 11.1): (1) temporal variability, (2) temporal determinism, and (3) temporal predictability. Temporal variability is most typically measured as the standard deviation of the environmental records in a time-series. From a mathematical standpoint, temporal variability is not independent of the time-series' mean and does not account for temporal periodicities. The two additional axes, temporal determinism and temporal predictability, can be represented by dynamical measures calculated using the approach of Recurrence Plots–Recurrence Quantification Analysis (RP–RQA). Determinism is the reciprocal of stochasticity. Temporal determinism represents the percentage of all recurrences in the RP that are part of diagonal lines. A diagonal line is one that contains two or more recurrences forming an uninterrupted sequence running parallel to the line of identity; i.e., the longest diagonal line splitting the RP in two halves. Determinism will be zero if all recurrences are single dots. The second measure, temporal predictability, represents the average forecasting horizon of the system states and is expressed in time units. Temporal predictability is calculated as the mean of the frequency distribution of diagonal lines in the RP, excluding the line of identity.

Other RP–RQA measures, such as the tendency of records in time-series to drift away from the long term mean (*Trend*; [8]), may also be useful for characterizing transiency in ecological and climatic dynamics (see Chap. 12). In general, the recurrence plot approach provides alternative ways of describing dynamical systems but is not without its own shortcomings. RP–RQA measures cannot be interpreted beyond sampling limitations in terms of missing data, time-series length and temporal resolution. These limitations are discussed in detail in Marwan [14].

11.4 A Case Study of Climate–Biodiversity Relationships

11.4.1 Context

The relationship between climate and biodiversity is one of the most pervasive patterns of community ecology. Several studies, covering a range of ecosystems, have shown that large-scale geographic variations in taxonomic biodiversity correlate to energy- and water-related climatic variables (reviewed in [15, 16]). Over large geographic distances, the variation in plant and mammal biodiversity has been associated to the long-term mean or temporal variability of temperature and precipitation (e.g., [17–20]).

Non-spatial competition models in community ecology suggest that, unless environmental conditions vary unpredictably, even small functional differences among species may eventually lead to competitive exclusion (e.g., [4, 21]). Thus, one could hypothesize that lower levels of temporal determinism and predictability in climatic dynamics may slow the rate of competitive exclusion, allowing more species to coexist. Lower climatic predictability would thus translate into greater environmental heterogeneity in time, creating more opportunities for species coexistence.

In this case study, we explore the validity of this premise through the use of RP–RQA measures to quantify temporal determinism and predictability in climatic time series. We then explore the relationships between biodiversity and climate dynamics at different locations along a north–south gradient. For the first time, these relationships will be contrasted against those obtained using conventional measures of climatic dynamics (i.e., long-term mean and standard deviation).

11.4.2 Methods

We used as biodiversity variables the number of mammal species [22] and angiosperm tree families [18] over the North- and South-American landmasses at a resolution of 1° and 2°, respectively. We extracted monthly climatic time-series from the global dataset compiled by the Climate Research Unit on grid-cells of 0.5°, for the period 1920–2002 (CRU TS 2.1; [23]). We then calculated the mean and standard deviation of monthly temperature (°C) and precipitation (mm) time-series. Finally, we built two recurrence plots (RPs) for each grid-cell, one for monthly temperature and the other for precipitation. Following von Bloh et al. [6], we chose an embedding dimension of $m = 3$, a time-delay of $d = 1$, as well as adjustable threshold values (*thresh*) allowing us to fix the recurrence rate to 10 % in the RPs. We used the CRP Matlab toolbox [8] to calculate temporal determinism and predictability measures.

For each climatic variable (temperature and precipitation), we spatially averaged the measures of determinism, predictability, mean and standard deviation at the grid-cell resolution of each biodiversity dataset. We graphed bivariate climate–biodiversity relationships and calculated their coefficient of determination (R^2) using recursive trees. A recursive tree is comparable to a regression model without the statistical assumptions of linearity and normality of the predictors. Recursive trees were fitted using the R package “rpart” version 2.15.3 [24].

11.5 Results and Discussion

The three dynamical measures—temporal variability, determinism and predictability measures—were weakly correlated with each other for the precipitation data (Fig. 11.2a), suggesting that determinism and predictability contain important dynamical information not captured by the standard deviation. The highest association was between determinism and predictability (Pearson’s $r^2 = 0.46$) and the lowest between determinism and variability (Pearson’s $r^2 = 0.13$).

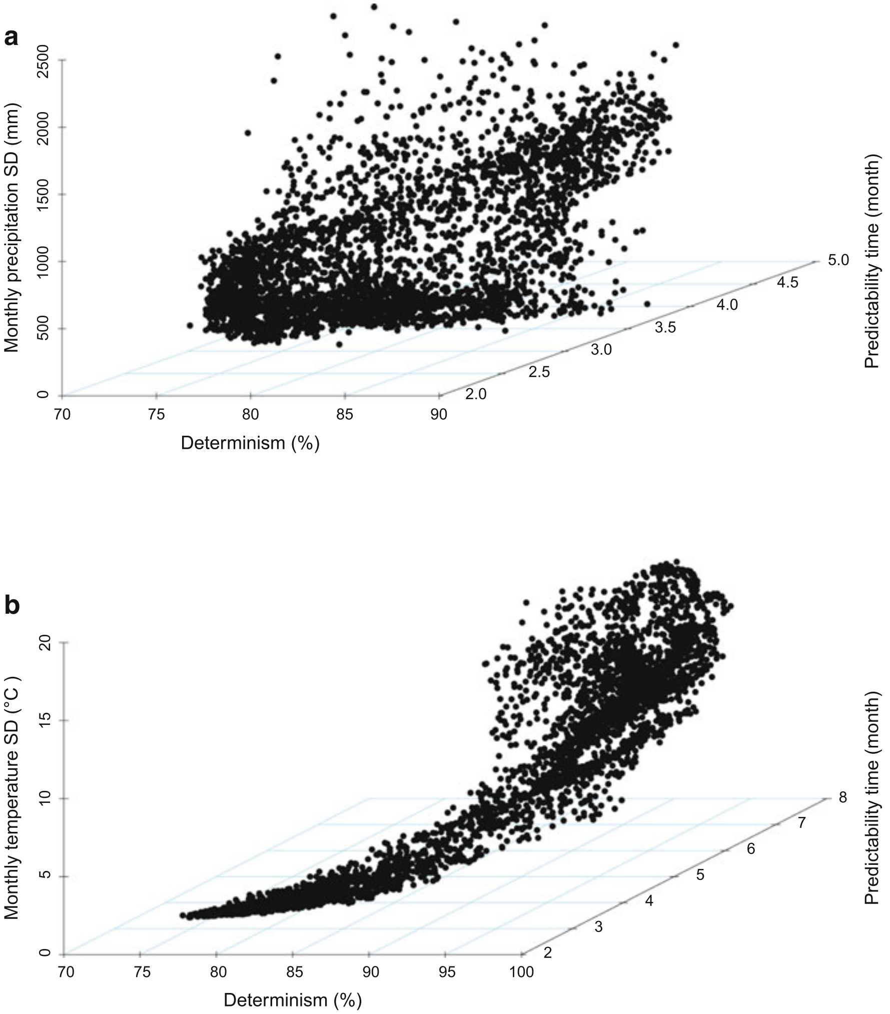

Fig. 11.2 Relationships among measures of temporal variability (standard deviation; SD), determinism and predictability for (**a**) precipitation and (**b**) temperature data. Monthly climatic time-series covered the period 1920–2002 at a spatial resolution of 0.5° over North- and South-America. Each point represents one location

In comparison, the three measures were rather strongly correlated for the temperature data (Fig. 11.2b), with the highest association between determinism and predictability (Pearson's $r^2 = 0.85$) and the lowest between predictability and variability (Pearson's $r^2 = 0.66$).

Bivariate biodiversity–climate relationships for the two datasets revealed contrasting patterns (Fig. 11.3), extending from none (e.g., mammal species richness vs precipitation determinism.) to strongly linear (e.g., mammal species richness

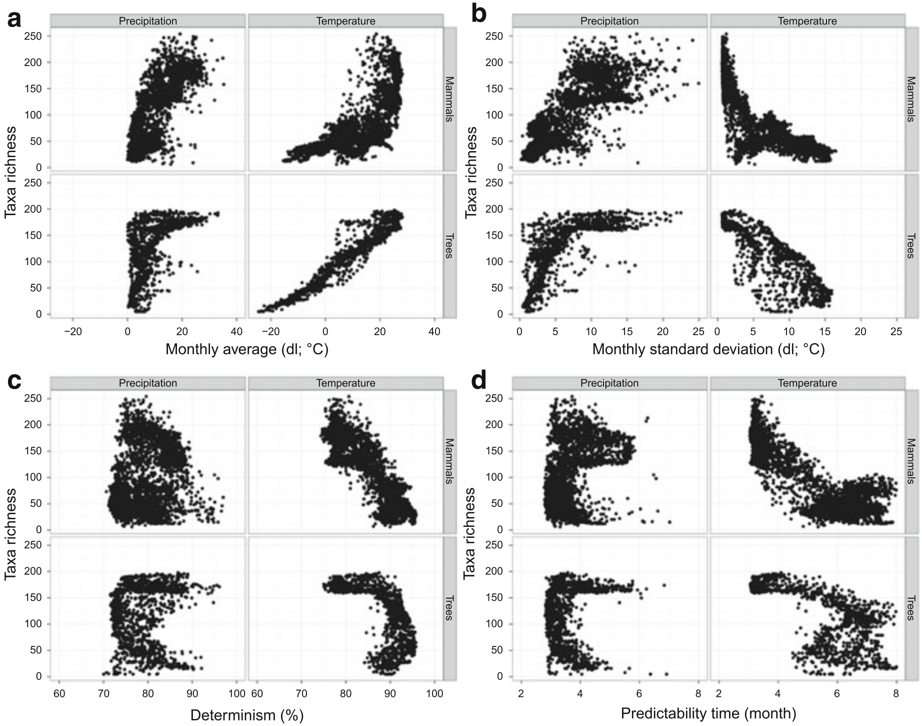

Fig. 11.3 Relationship between dynamical measures of climatic time-series (temperatures, precipitations) and taxonomic richness (mammal species, tree families) for North- and South-America. Figure panels show the relationships with: (**a**) long-term mean (monthly average), (**b**) temporal variability (monthly standard deviation), (**c**) temporal determinism (%) and, (**d**) temporal predictability (average forecasting length in months). Monthly mean and standard deviation measures of precipitation data are expressed in decilitres (dl). In each panel, *left* and *right* columns show relationships to precipitation and temperature data, respectively, whereas *top* and *bottom* show relationships to mammal species richness and tree family richness, respectively

vs temperature mean.), and including asymptotic (e.g., tree family richness vs. precipitation standard deviation) as well as more complex functions (e.g., tree family richness vs. temperature predictability). Both the number of mammal species and tree families were positively related to long-term averages of monthly temperature and precipitation time-series (Fig. 11.3; panel A). No such generality existed for the other variables, although some patterns can be observed (Fig. 11.3; panels B–D). At higher biodiversity levels, taxonomic richness decreased with increasing temporal variability, determinism and predictability of monthly temperatures. In comparison, richness related positively to the temporal variability of monthly precipitation, especially at lower biodiversity levels (Fig. 11.3; panel B).

How then might the global geographic distribution of biodiversity relate to the determinism and predictability of climatic variables? Our preliminary findings suggest that biodiversity increases with increasing temperature stochasticity and decreasing predictability, at least in the upper range of biodiversity values. Hubbell [25] suggested that species can coexist because they are essentially indistinguishable from one another in their realized demographic traits; that is the long-term persistence of species is independent of per capita birth–death rates. Subsequent tests have detected differences, although they are probably small (e.g., [26]). Alternatively, Clark et al. [27] proposed that species coexistence is possible because individuals within species differ and interact with their environment in many different ways. Maintenance of biodiversity in the above theories requires that, independently of the specific mechanisms involved, within-species variability in demographic traits is large in comparison to between-species variability (i.e., that ecological niches are high-dimensional). Both theories thus suggest a tight coupling between the dimensionality of ecological niches and environmental dynamics.

In atmospheric sciences, high-dimensional climatic systems are typified by dynamical measures of low temporal determinism and predictability [28]. Species may have higher-dimensional ecological niches if their resources respond to varying (e.g., less deterministic and predictable) climatic conditions, providing more opportunities for the niches of species to be distinguished [21]. Consequently, species may show different responses to their common varying climate and experience strongest intraspecific competition when favored by the environment, thus buffering population growth. This equalizing mechanism of species coexistence has been termed the "storage effect" (e.g., [21]). The storage effect has received support in a recent study by Usinowicz et al. [29] who showed that coexistence in tropical forests is facilitated through asynchronous variation in seed production among tree species. Runkle [30] had previously argued that the storage effect could explain the latitudinal gradient in forest diversity because in his own words: "Winter decreases effective environmental variation and imposes a synchronization in seasonal phenology upon species of trees in temperate zones. Therefore the probability that a rare species may encounter the unusual favorable period which will enable it to persist in the community is reduced". It remains to be examined if latitudinal differences exist in the strength of the storage effect.

The multiplicity of climate–biodiversity relationships seems to call for a multiplicity of hypotheses, but this may only confound the search for a general

Table 11.2 Coefficients of determination (R^2) calculated from the recursive trees fitted to each bivariate climate–biodiversity relationship

	Precipitation		Temperature	
Measure	Mammal species	Tree family	Mammal species	Tree family
Long-term average (Mean)	0.617	0.461	0.723	0.912
Temporal variability (SD)	0.701	0.687	0.831	0.739
Temporal determinism (DET)	0.123	0.054	0.802	0.438
Temporal predictability (L)	0.219	0.049	0.809	0.528

mechanism. When considering only the bivariate relationship strengths, one might conclude that mean temperature controls the number of tree families in the Americas, but that the geographic distribution of mammal species richness is determined by temporal dynamics in temperature (Table 11.2). In fact, 12 of the 16 measures of climatic dynamics were associated to nearly, or more than, 50 % of the geographic variation in biodiversity (Table 11.2). When the eight climatic variables were included in a model of recursive partitioning, the coefficient of determination attained values of 0.882 (88 %) and 0.922 (92 %) for mammals and trees, respectively. In models considering only the variables of mean precipitation and mean temperature, the coefficient of determination was distinctly lower for mammals ($R^2 = 0.785$), but only slightly lower for trees ($R^2 = 0.912$).

Alternatively, the multiplicity of relationships may indicate that biodiversity is constrained by more fundamental climatic processes, such as the latitudinal gradient in solar radiation dynamics. At the global scale, yearly solar irradiation at the top of the atmosphere is strongly negatively correlated to absolute latitude. Solar irradiation on Earth defines the maximum amount of energy that can, ultimately, be transformed into biomass and shared among species (the species-energy hypothesis; e.g., [15, 16, 31]). Moreover, latitudinal differences in solar heating drive the vertical and horizontal motion of air masses, which in turn entrain the broad-scale temporal dynamics in temperature and precipitation. Thus, over large geographical regions, different climatic variables may all relate to the same underlying variable, solar irradiation. In partial support of this idea, if we enter only the latitude coordinates of grid-cells in a recursive tree model, the coefficients of determination we obtained were as high as $R^2 = 0.857$ and $R^2 = 0.934$ for mammals and trees, respectively.

In summary, we found evidence that higher biodiversity levels of two taxonomic groups are associated with lower values of predictability, determinism, variability and higher long-term means in monthly temperature data. Our results also revealed a multiplicity of climate–biodiversity relationships, suggesting that identifying the specific mechanisms of large-scale geographic variations in biodiversity may be more complex that originally envisioned. In this context, the study of Nevo [32] is instructive as he compared the biodiversity of a large number of plant and animal taxonomic clades on two opposite south- and north-facing slopes at the Evolution Canyon in Mount Carmel, Israel. He found that plants (angiosperms) and animals (many insect and arthropod groups, reptiles and birds) were more diverse on the south-facing slope than on the north-facing slope. Genetic diversity was also higher on the south-facing slope. Nevo described the south-facing (high biodiversity) slope in the following words: "… warmer and drier (receiving up to 300 % more solar radiation), micro-climatically less predictable than the north-facing slope". He added: "The south-facing slope represents a 'spatiotemporally broader niche' …" [32]. We propose that representation of a spatiotemporally broader niche may be extended to include large-scale variations in climate dynamics.

11.6 Perspectives

The RP–RQA approach can contribute to the investigation of other research hypotheses in community ecology. For example, the mismatch hypothesis (e.g., [33]) states that the survival of populations and communities is impaired if ecological processes, such as plant greening and flowering, animal migration, or breeding events, are desynchronized over time. Loss of seasonal or inter-annual predictability in the timing of climatic events is known to be detrimental to the functioning of plant and animal species [34, 35]. In this context, the vulnerability of communities to temporal mismatch may depend on the predictability of climatic and ecological processes. Temporal mismatch between ecological and climatic processes could be readily assessed with the approach of cross-recurrence plots (CRP; [8]).

Another hypothesis posits that species-rich communities host a variety of life strategies that respond differently to environmental conditions and contribute to ecological functioning in different ways, thus increasing the temporal stability of ecosystems (e.g., [36, 39]). Considering that the concept of stability is necessarily multifaceted, different measures of temporal variability, determinism and predictability are needed to uncover the mechanisms of biodiversity–stability relationships. For example, using a multi-species competition model with environmental forcing, Proulx et al. [10] found a positive biodiversity–stability relationship when community stability was defined using measures of temporal determinism and predictability. No such relationship was observed when measures of temporal variability were used to define community stability [10]. Multivariate recurrence plots (MRP; [37]) can be used to calculate measures of temporal determinism and predictability of dynamical systems with many interacting variables.

In conclusion, recurrence plots and recurrence quantification analysis hold promise for describing and detecting dynamical patterns in ecological time series. They provide a simple alternative to other methods of non-linear analysis (e.g., attractor reconstruction, Lyapunov exponents, correlation dimension analysis) that require long time series and have rarely provided convincing results for ecological data (e.g., [38]). In contrast, the RP–RQA approach provides a more subtle description of determinism and predictability in a time series, and thus may prove more useful than other approaches for detecting deterministic structure in ecological data. Ecological systems have a dynamic that is inherently non-linear; however, many quantitative methods in ecology ignore this fundamental aspect of the time series to which they are applied. RP–RQA thus provides a good complement to the ecologist's quantitative toolbox.

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