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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOULÇÃO DA BIODIVERSIDADE
MESTRADO EM ECOLOGIA E EVOLUÇÃO DA BIODIVERSIDADE
MARCO MIGUEL ODICIO IGLESIAS

COMMUNITY AND SPECIFIC-SPECIES LEVEL RESPONSES TO ENVIRONMENTAL CONDITIONS OF THE SNAKES OF A COASTAL DUNE ECOSYSTEM IN SUBTROPICAL BRAZIL INFERRED FROM A NINE YEARS TEMPORAL GRADIENT

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PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL

FACULDADE DE BIOCIÊNCIAS

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Dissertação apresentada como requisito para a obtenção do grau de Mestre pelo Programa de Pós-Graduação em Ecologia e Evolução da Biodiversidade da Escola de Ciências da Saúde e da Vida da Pontifícia Universidade Católica do Rio Grande do Sul.

Marco Miguel Odicio Iglesias

Orientador: Santiago Castroviejo Fisher

DISSERTAÇÃO DE MESTRADO
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RESPOSTAS DA COMUNIDADE E ESPECIES ESPECÍFICAS ÀS CONDIÇÕES AMBIENTAIS DE UM GRADIENTE TEMPORAL DE 9 ANOS, EM UM ECOSSISTEMA DE DUNAS NO BRASIL SUBTROPICAL

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RESUMO

O ecologista pode intuitivamente pensar que as respostas aos distúrbios no nível da população aumentam para impactar as propriedades no nível da comunidade. No entanto, há evidências experimentais e empíricas que sugerem que grandes respostas a distúrbios no nível da população não necessariamente se traduzem em mudanças equivalentes no nível da comunidade. Investigamos se a composição da comunidade de serpentes e a abundância de espécies específicas mudam ao longo do tempo e se essa mudança pode ser explicada pelas condições ambientais, ao mesmo tempo, vemos se tanto a comunidade quanto a população têm respostas equivalentes a essas mudanças. Para tal, trabalhamos no mesmo ecossistema de dunas costeiras (<444 hectares) numa escala temporal, entre 1998-2004 e 2020-2021. Nossos resultados mostram que a comunidade e quatro espécies de serpentes diminuíram ao longo do tempo. A redução na composição da comunidade ocorreu nos últimos períodos (2020-2021) quando comparado há 15 anos, com o último período de 2004. No nível comunitário, as variáveis ambientais explica pouca variações na composição, enquanto a variável de correlação temporal positiva atua como fator dominante, sugerindo que a redução na comunidade não pode ser explicada por modelos ambientais. Ao nível populacional, foi detectado um caso de diminuição na serpente *Xenodon dorbignii* e uma tendência negativa de diminuição de três espécies. Em geral, as variáveis ambientais foram positivamente correlacionadas com as abundâncias e não podem explicar o padrão de declínio nas serpentes. Nas dunas costeiras, tanto a comunidade como a população respondem da mesma forma.

PALAVRAS-CHAVE: Dunas costeiras, correlação temporal, composicao da comunidade.

ABSTRACT

Ecologist may intuitively think that responses to disturbances at the population level scale up to impact community-level properties. However, there is experimental and empirical evidence suggesting that large magnitude responses to disturbances observed at the population level do not necessarily translate into equivalent changes at the community level. We investigate if snake community composition and the abundance of specific-species change across the time and if this change could be explain by environmental conditions, at the same time, we see if both community and population has equivalent responses, to those changes. To this, we work in a same local of coastal dunes ecosystem (<444 hectares) in a temporal scale, between 1998 – 2004 and 2020 -2021. Our results show that community and four species of snake decreased across time. The reduction of community composition was in the last periods (2020-2021) when was compared 15 years ago, with the las period of 2004. At community level, environmental variable explains a few variances of composition, whereas positive temporal correlation act as a dominant factor, suggesting that reduction on community cannot be explain by environmental models. At population level, we detected a confirm case of decreased in the snake *Xenodon dorbignii* and negative tendency on decreased of three species. Overall, environmental variables were positively correlated with the abundances, and cannot explain the decreased patron on snakes. In coastal sand dunes, both community and population responses in the same way.

KEY WORDS: Sand dunes, temporal correlation, species responses, community composition.

PRESENTACIÓN

Disminuciones en poblaciones de Squamata son difíciles de detectar, y estudios de larga data son considerados indispensables para entender tendencias y fluctuaciones poblacionales. Sin embargo, la mayoría de estudios son de corta duración, útiles para determinar el estado actual de las poblaciones pero no para documental variaciones en el tamaño y la salud [1]. Baja detectabilidad y densidad combinado combinadas con cuestiones taxonómicas complejas, comunidades muy diversas pero con limitaciones logísticas, se encuentran entre las primeras razones detrás de esto. En las dunas costeras de Brasil se encuentran comunidades de serpientes particularmente ricas en especies con altos niveles de endemicidad, pero se sabe poco sobre los mecanismos detrás de estos patrones [2–4]. Por otro lado, las áreas costeras de dunas experimentan altas tasas de disturbios naturales y antropogénicos [5]. Entro los problemas más serios de estos ambientes, se ha señalado la invasión de especies, el uso de tierras [6]. Debido al calentamiento global, se esperan eventos de enfriamiento extremo más frecuentes durante el clima invernal en latitudes medias y regiones subtropicales [7] y esto aparentemente está causando un aumento en la cobertura vegetal de las dunas costeras globales [8]. En este escenario, nosotros proponemos estudiar como comunidades de serpiente y algunas poblaciones responden a estos cambios ambientales. Nosotros nos preguntamos si respuestas a nivel de comunidad pueden ser generalizados al nivel poblacional. Para ello, estudiamos la variación en la composición de la comunidad y abundancia de especies específicas en un periodo continuo de años entre 1998 – 2004 y 2020-2021. Al mismo tiempo, evaluamos si posibles cambios en la comunidad y población pueden ser explicado por variables ambientales que caracterizan las dunas (i.e., aumento de áreas urbanas, velocidad de viento, crecimiento o disminución de vegetación de pastizales). Estas preguntas serán dirigidas en un único artículo, considerando dos secciones 1) cambios en la composición y su relación con variables ambientales y correlación temporal, 2) tendencias en la abundancia de especies específicas y su respuesta cambios ambientales.

RESEARCH ARTICLE

Community and specific-species level responses to environmental conditions of the snakes of a coastal dune ecosystem in subtropical Brazil inferred from a nine years temporal gradient

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Introduction

Because both organismal populations and communities are logically connected due to the hierarchical ecological structure—communities are composed by species populations—, ecologist may intuitively think that responses to disturbances at the population level scale up to impact community-level properties. However, there is experimental and empirical evidence suggesting that large magnitude responses to disturbances observed at the population level do not necessarily translate into equivalent changes at the community level [1,2]. This is because community level properties, unlike specific-species ones, may still be maintained by extinction or decline compensatory mechanisms [3]. Consequently, it is widely accepted that community composition is a necessary response variable to estimate the impact of changes in ecosystems, natural or anthropogenic. At the same time, any given community could be temporally structured by induced temporal dependent mechanisms [3–5]. Thus, environmental and temporal dependence can jointly explain changes in community dynamics.

Coastal lands are particularly exposed to disturbances due to the influence of oceans and human activities, providing excellent natural experiments. The transition of the terrestrial-aquatic systems creates unique geomorphological and climatic conditions within these areas that may increase long and short-term disturbances. For example, tides, hurricanes, sea level fluctuations, and subduction zones. Simultaneously, while coastal areas account for only 20 % of all emerged land in the world, it harbors 41 % of the world population, placing more infrastructure and associated economic investment on the coast and therefore, increases human impact on coastal ecosystems [6].

Coastal dunes are a good example, as they experience high rates of natural and anthropogenic disturbances[7]. Invasive plants (exotic or native) and land use have been identified among the most serious problems [8]. However, due to global warming, more frequent extreme cooling events are expected during winter weather in mid-latitudes and subtropical regions [9] and this is apparently causing an increase of cover vegetation of global coastal dunes [10].

Within coastal dunes, snakes constitute key components of their vertebrate fauna due to their role as predators, sensitivity to abiotic and biotic changes (natural or anthropogenic), large variation in ecological and life history traits among sympatric species (e.g., adult body sizes, dietary habits, and reproductive biology), and poikilothermy and sensitivity to climatic variables [11,12] The Brazilian costal dunes harbors particularly species rich communities of snakes with high levels of endemicity, but little is understood about the mechanisms behind these patterns [13–15]. Thus, these snake assemblages of the Brazilian coastal dunes constitute excellent natural experiments to study community and specific-species responses to changes on environmental conditions over time.

Considering this context, we quantified environmental and climatic variables of a coastal dune ecosystem in subtropical Brazil together with community and population species measures of its snakes for a 9 years period. At the community level, we tested if: (i) snake composition changed and decreased across time periods, and (ii) these changes could be explained by environmental conditions and temporal dependence. We also evaluated if specific-species responses accompanied those at community level by testing if: (iii) species specific-abundances changed across time, and (iv) this changes could be explained by environmental variables.

Materials and methods

Study area

We collected data in a locality within the sand-dunes of Magistério municipality (30°21’S, 50°17’W), state of Rio Grande do Sul, Brazil from 1998 to 2004 and 2020 -

2021 (Fig 1). The study area is part of the southern Atlantic Ocean coast of Brazil and is about 1km from the shore and just a few meters above it. The climate is subtropical (Köppen 1936), with a mean temperature of 15.4 °C (minimum and maximum monthly average 12.2 and 18.3 °C, respectively). The area is subjected to intense solar radiation and strong wind action that originates mobile dunes interspersed with small depressions [16]. Vegetation cover is spread and scarce, predominating species are *Andropogon arenarius, Hydrocotyle bonariensis, Panicum racemosum, P. sabulorum,* and, *Spartina iliate* [17]. Depressions between the dunes accumulate organic material and are flooded during the period of greater rainfall, allowing the grow of hydrophytes species such as *Juncus* sp., and cyperaceous plants. The area is surrounded by two permanent lagoons (Cerquina and Rincão das Éguas). Human activities are part of the landscape, with urban areas, roads, and plantations of *Pinus* sp. The area is used by feral and domestic dogs, horses, and tourists. There is illegal sand extraction near the urban areas, although apparently occasional.

Sampling design and field data collection

We visited the same location to detect and capture snakes using a visual encounter survey technique [18]. We walked through the mobile sand dunes and their boundary with grasslands, pine plantations, urban areas, and temporal lagoons. Roberto Baptista de Oliveira (RBO) led and performed surveys from July 1998 to June 2004, while RBO and Marco Odicio-Iglesias shared responsibilities from October 2020 to December 2021. We sampled during day and night hours in the 1998–2004 period and only during the day in 2020–2021 to avoid conflicts with locals caused by recent invasions of the dune areas. We identified each captured snake to the species level and recorded its mass, with a precision scale, snout-vent-length (SVL), and tail length (TL), both with a tape measure. We also sexed all specimens by everting their hemipenes. Immediately after recording these variables, we released the specimen at its site of capture. We carried out surveys throughout the entire year. However, we maximized our sampling effort in the spring (September to November), which is the period of highest activity and, consequently, detection.

Because we started surveys in June 1998, we defined six initial consecutive time periods of 12 months, each starting on June (winter) and finishing in May (autumn) of the next year. Hereafter, we refer to this time periods as periods 1 to 6 (Table 1). After May 2004, sampling became more erratic due to constrains in resources. This eventually led to a 15 years gap (2005–2019) without sampling and delimitation of sampling periods of 7 instead of 12 months (Table 1). As we started each period in winter, we considered this division to account for the intra-period variation of the community composition or species abundances, at the same time, we expected that if environmental variables have an effect on snakes, this could be naturally detected, because snakes failed to survive the following winter.

During these nine sampling periods, we searched for snakes a total of 612 days, with the average number of sampling days per month within each period being 4.0–9.3 days. We used each month as the sample unit, and we estimated sampling effort in numbers of days and accumulate minutes per month (Tables 1 and S1).

Quantification of environmental conditions

We used 14 variables that are a combination on environmental and land use and cover to quantitatively characterize the sampling area (Table 2). Herein, we used environmental variables (EN) as conditions and resources related to habitat, climate, and soil. These are important for establishment and survival of organisms and have been used as significant predictors of species diversity and ecosystem function [19,20]. Land used and cover are factors that play a meaningful effect in changing environmental conditions [21] and we used a combination of urban increment and sand dunes reduction to summarize the effect of urbanization on the study area [22]. We obtained all variables for each month from 1998–2004 and from 2020–2021, matching our sampling effort.

To quantify variables, we previously define the study area spatiality, as a polygon of 420 hectares, which represents the area where we started our study in 1998 to 2021 (Fig 1). We delimited the area in the field by walking around with a Global Positioning System (GPS Garmin eTrex) using the track function to map the entire area. Then, we defined a polygon using Quantum Geographic System Information (QGIS) 3.16.11.

We obtained data for all variables using the Google Earth Engine cloud computing environment (hereafter, GEE), and the R software, which reduced computational efforts. Within GEE, we used two climatic global datasets to extract environmental records at 5000 and 11000 m of resolution, respectively (available at the Earth Engine Data Catalogue). We used a collection of Landsat Images 5, 7, and 8 to compute specific indexes for climate, habitat, and urbanization with 30 m resolution, cloud cover > 30 %, and a cloud masking function for each image. Briefly, our procedure to calculate variables was: 1) to import the study area polygon to the cloud assets section in the GEE platform; 2) to export the area into the GEE Code Editor application and define the desired period of time [23]; 3) to select the dataset image collection of interest and filter the study area, 4) to select the variables of interest (e.g., "precipitation") and define a reference point for the extraction of the dataset into the area, 5) to export the results as a table to Google Drive. When we worked with Landsat Images collections, we used a specific extraction protocol designed by Ermida *et al.* (2020) [24] and built our specific code to perform a temporal analysis series using specific band images to compute specific variables. Additionally, we estimated urban land use and proportion of sand dunes and grassland for the study area and for each year. For this, we classified the study area in four landscape classes: 1) sand dunes; 2) grasslands; 3) urban; and 4) pines. We later quantified the proportion of the total area (420 hectares) of each of these classes through time. For this, we developed a supervised classification using the package Classifier with the algorithm smileCart available in GEE using the following workflow: 1) to select Landsat Images 7 and 8 and define a period of time, 2) to reduce the collection of images for each period of time, 3) to collect spatial data for each landscape class using the study area as the point of reference and training the classifier algorithm; 4) to run the classifier algorithm and map geometrically each landscape class into the study area; 5) to estimate the classification accuracy of the model by separating 70 % of our dataset, and perform a new classification test to estimate the Kappa index. We considered a Kappa index > 90 % of accuracy for each year, and 6) to transform the classified image into a vector file and export it in shape format. We used QGIS 3.16.11 version[25], to estimate area surface by each class in hectares.

We used historical monthly weather data from WorldClim [26] and downloaded the average minimum and maximum temperature (C°) at 2.5 minutes (~21 km^2), the spatial resolution in GeoTiff (.tif) files format for 1998–2004. Then, we used a script in R to obtain the temperature dataset for study area. For 2020–2021, we obtained temperature data from Tramandai Climatic Station (~21 km away from the study area: -30.01, -50.13). We downloaded data from the online platform of the Rio Grande do Sul National Institute of Meteorology, which has data available since 2000. Tramandai station has similar conditions to the study area because is part of the coastal dune ecosystem. The code to obtain the dataset of environmental variables is available in Appendix S1.

We performed the variance inflation factor (VIF) to detect multicollinearity among the 13 set of variables. We used VIF > 5 as a threshold to drop variables and retained those that could provide better explanatory power based on the study system [27].

Data analysis

Quantification of community composition variation

We estimated the level of dissimilarity composition between pairs of each snake species. First, we performed an optimal dissimilarity measure analysis using a classical multidimensional scaling (MDS) of our abundance matrix to visualize the distribution of abundances across a two-dimensional scale. We compared the six commonest abundance indexes used in ecology for this type of data. We used the *cmdscale* function to create a matrix distance with each of the six methods (“Bray Curtis”, “Euclidian”, “altGower”, “Manhattan”, “chisq”, “Camberra”). Based on these results, we selected the Bray Curtis index because it shows no pattern in the dispersion of the data (Fig. S1). To visualized patterns of community composition groups, we used non-metric multidimensional scaling (NMDS), an indirect gradient analysis, based on our Bray Curtis dissimilarity result. Previously, we made a comparation between NMDS and Principal Coordinates Analysis (PCoA), using the *cor* (Spearman Correlation) function, to evaluate the degree of correlation between those methods and our dissimilarity index. NMDS had a higher spearman correlation than PCoA (0.933 versus 0.811, respectively, Fig. S2). Accordingly, we used NMDS as an ordination method to visualize and test changes in community composition.

Change probability in community composition

To detect changes in community composition, we used the NMDS results, and a multivariate normal t-test analyzed with a Bayesian approach through a Markov chain Monte Carlo (MCM) as implemented in R and JAGS. We evaluated through progressive pairwise comparisons between temporal sampling periods: (i) the probability of change of snake community composition by comparing the centroids of standard ellipses, and (ii) the probability of the composition directionality (i.e., decrease or increase) by using the area of the standard ellipses. For this, we used the model of community composition ordination analysis built by Zipkin *et al.* (2020) [28]. Briefly, we created a matrix in which we coded the pooled number of encounters per month per sampling period for each species.

Each comparison only considered species that were recorded within each sample. We compared groups of pairwise years as an ordered series relative to time (i.e., periods 1 and 2, 2 and 3, so on). It is important to highlight that we have a 15 years gap without sampling (2005–20019) separating periods 7 and 8. We performed NMDs in a range of 1 to 4 dimensions to look for a low stress value (0.09) and a good representation of ordination spaces [29]. To perform this analysis, we used the *metaMDS* function (with arguments k = 1 or 4, distance= “bray”, try=1000, trymax = 10000) and extracted the estimates for each visit. NMDS points closer in a phase space have more similar community composition than points further apart. We used the extracted values to run a multivariate normal t-test to evaluate if the mean and variance of the two-dimensional points for each visit differed between pairwise comparisons[28]. Then, we used the covariance matrix and centroid mean estimates to create standard ellipses for each period with the ellipse package in R[30].

Temporal correlation on community

The temporal structure of our dataset was expected to produce temporal dependence processes in community composition. To account for it and test for potential mechanisms that induced temporal dependence by environmental control [4], we applied distance-based Moran's eigenvector maps (dbMEM) for our irregular time series. We used temporal observations to compute a series of sine waves. Prior to it, we examined if our response variables had a linear correlation with time coded as months. We considered the results ($p < 0.001$, $R^2 = 0.0519$) as non-problematic due to the low predictive power of the linear model.

We computed a distance matrix among time observations (as spatial coordinates) and determined a truncation threshold (*thresh*) considering irregular series. We used the length of the largest lag as the threshold value multiply by 4 on the diagonal of the distance matrix as recommended by [4]. Then, we computed a PCoA of the truncated distance matrix that describes which observations are considered neighbors and which are not. This produced the eigenvectors of the Gower-centered distance matrix that are the Moran's eigenvector maps forming matrix T (*time*). In our irregular time series, the first half of eigenvectors have positive eigenvalues and model positive temporal correlation. The second half have the negative eigenvalues as a negative temporal correlation. We used the function dbMEM with arguments (xyORdist = [distances matrix of dates], thresh = [16*4], MEM.autocor = "positive [or negative]). Then, we computed a redundance analysis (RDA) between the community composition data set and the estimated positive and negative dbMEM. We performed variance analysis (anova) to determine the importance of the temporal correlation model (positive and negative) over the response data (community composition) and R^2 to measure size effect. We also computed Anova for each RDA axis to determine its contribution to community composition. Furthermore, we performed a forward selection by permutation of multivariate residuals only considering dbMEMs (*temporal correlation variables*) with p-values < 0.05. We used the significant variation of the dbMEMs axis in a linear regression model by stepwise selection using the aforementioned environmental variables as a pool to explain variables. We tested for normality for each regression model of residuals using the Shapiro test.

Community responses

We linked the temporal correlation with environmental conditions to evaluate their influence on community composition pattern. As a first step, we performed a forward selection analysis of the seven environmental variables to select for statistically significant ones for the VP analysis. Then, we used the fitted values of the previously selected dbMEMs ($p < 0.05$) and the selected environmental variables in a variation partitioning analyses (VP). This way, we partitioned the variation of the response variable among two or more sets of explanatory variables using series of regressions. The adjusted R^2 of the analyses are then combined to calculate the amount of variation explained by each explanatory variable and their shared variance [31]. We used VP analysis to discriminate the influence of environmental variables by considering each variable individually or in two classes (i.e., habitat and climate). When individual fractions of variance were obtained, we tested for significance ($p < 0.05$) using RDA and *anova* tests. We could not test for significance of join effects as they cannot be directly computed by canonical analysis.

To perform all statistical analysis in temporal correlation and community responses sections we used the *adespatial* [32], mvpart [33], packfor [34] the vegan[35] packages and the custom function R2.by.variable [4], in the R environment[36].

Quantify variation on specific-species abundances

We study if the abundances of the most sampled species vary across periods in the study area. Specifically, we study if (i) individual species show a trend across periods (i.e., decreased or increased) and (ii) environmental variables are related to the changes and good predictors. We focused exclusively on the most sampled species to reduce the impact of small sample size. We started by testing the distribution model that better fit the data and found that the Poisson and Negative Binomial distributions were good predictors. Whenever possible, we used the Negative Binomial distribution because the variance for each species was larger than mean. However, we used the Poisson distribution for some analyses because of their assumptions. Because we have different sampling efforts per month among periods, we modelled the number of days and accumulated minutes as predictive variables of number of counts in each month (92 observations). For this, we used Generalized Additive Models (GAM) with a smooth function of predicted variable, modelling each predictive variable separately. To determine the best linear tendency relationship, we used the significance of smooth function ($p < 0.05$) and the highest R^2 confront the two models. This relationship was then included into the models as *offset variable*, to indicate that some proportion of variances on counts are affected by the effort.

To test trends on species abundance and to account for temporal correlation and heterogeneity (i.e., evident pattern among residuals versus fitted values), we first applied a generalised least squares (GLS) model without correlation structure so that we had a reference point. Then we used Generalized Lineal Mixed Model (GLMM) to reduce the temporal correlation and heterogeneity among our samples, using a random structure. In both models, we used count data as response variable and periods (1–9) as a predicted nominal variable. With the GLS, we assumed a non-parametric model, and with the GLMM model we used a negative binomial distribution. We submitted each GLMM fitted model to a validation process to confirm if it complies with underlying assumptions following the guidelines described in [27,37]: 1) to estimate the dispersion statistic of fixed effects, 2) to plot the Pearson residuals versus fitted values, using each covariate included in the model, 3) to fit a GAM on the residuals with the predicted variable and check for a non-linear pattern, a $p< 0.05$, and $R^2 > 1\%$, 4) to plot an auto-correlation function (ACF) panel of residuals versus samples to see the values of the ACF at different time lags as an indicator of independence assumption of fit model, 5) to simulate 10000 datasets for each model from each analysis to estimate the number of zeros simulated by the model and plot them against the observed number of zero, if the number of observed zeros is within the simulated variation, the model complies with the data.

For each model, we used abundance of each species as a response variable and the time periods (1–9) as a nominal predictive variable plus the offset variable. Then we used GLMM to model temporal correlation with random structures, we test if combination of each observation (n=92), months and periods as a random effect reduce heterogeneity and the auto-correlation in our model.

To test if environmental variables could explain the abundance of each evaluated species, we used GLMMs models. Here, in some cases we used a Poisson distribution, because of parameters number of model could not convergence, using a negative binomial distribution. We test the abundance responses to each species, at Habitat and Climate scales. To this, we grouped variables to represent habitat (sand, grassland, vegetation index [NDVI] and season), all these variables are nominals. Then, we grouped Climate variables (Temperature, Wind and Precipitation), as continuous variables. With each group (Habitat and Climate) we apply a model selection process. Significant variables were select to each model and build a general model (Habitat + Climate) and again apply the selection process of this variables with the abundance. All these variables were included into the model as a fixed effect plus a random structure (i.e., 1|season, 1|month), that we test during the model selection and validation process.

The model selection was done following the guidelines in [39], this based on Diggle *et al.* (2002). We started with a general model without interactions, then we drop by one by individual variables with the least significant term ($p > 0.05$) and used AIC or

BIC to decide on the optimal model. During the process we used analysis of variance (ANOVA) to compare, AIC and p-values among the full model and reduce model. The R square were estimate as a “Marginal value” refers to fixed effect and “Conditional value” to all parameters (random and fixed effects).

To perform these analysis we used the nlme [40], lme4 [41], mgcv [42], MASS [43], PiesewiseSEM [44] packages in the R environment.

Results

We founded 14 species of snakes across period 1 and 9 (Table 3, S2 Table), five of them present across all sampling years: *Erythrolamprus poecilogyrus*, *Helicops infrataeniatus*, *Lygophis flavifrenatus*, *Philodryas patagoniensis,* and *Xenodon dorbignyi*. In general, community composition across the nine time periods by each month and season show a negative trend (Fig. 2).

As a result of the multicollinearity analysis among the 13 environmental and land use and cover variables, we selected seven variables with pairwise Pearson’s correlations ranging from -0.49 to 0.64 and VIF > 5 (Table 4). The variables Urban areas, Sand dunes, NDVI index, and Grassland show directionality across periods of time (Fig. 3).

Community composition variation across the time

Overall, the results of the community composition ordination analysis show that snake composition varied across time periods (Fig. 4). Pairwise comparison of standards ellipses during the initial years show a dynamic community composition (Fig. 4a-c), and that is more evident between periods 4 and 3 (Fig. 5c). The probability of standard ellipses reduction from pairwise comparisons between periods 7 and 4 is null (Fig. 5d-f). Conversely, the probability of reduction between periods 7 and 8 is high and similar to that detected for periods 4–3 (Fig. 5c, g). The pairwise comparison between periods 9–8 also shows a probability of reduction of similar magnitude (Fig. 5h).

Temporal dependence and environmental constraints

We find a positive temporal correlation, with a model containing 34 MEMs, that is globally significant ($R^2 = 0.22$, $p < 0.001$). The first RDA axis is significant for the positive temporal correlation ($p < 0.001$). A negative correlation model was not significant ($p > 0.05$). Consequently, we concentrated on modelling the positive temporal correlation to compute RDA of the community composition dataset with estimated positive MEMs. We selected nine MEMs by forward selection processes. These MEMs predict some unknown variation in the snake community composition across years ($p < 0.05$, Table 5). Except for one MEMs, they fluctuate considerably across the first block of time periods (1998–2004), conversely MEMs show a homogeneous composition during the last years (2020–2021) (Fig 5).

Based on these nine MEMs, the RDA model produce two significance axis that represent the positive correlation model relationship by all MEMs ($p > 0.01$, $R^2 = 0.18$) for snake composition. The linear regression analysis showed that the first RDA axis is explained by Urban area, Grassland vegetation, Wind, and minimum temperature ($R^2 = 0.41$, $p < 0.0001$). Furthermore, the first three variables have a negative estimate, indicating a negative relationship with composition. The second axis is only explained by Grassland vegetation, but the size effect is low ($R^2 = 0.07$, $p < 0.004$).

Variation partitioning of environmental variables and positive temporal correlation

We retained five environmental variables by forward selection: sand, NDVI, minimum temperature, wind, and evapotranspiration. Partitioning the variation of community composition with respect to these five environmental and the positive MEMs (derived from temporal correlations) variables explained 22.3 % of the global variation (Fig. 6a).

Both environmental and MEMs have a significant contribution ($p < 0.001$). The dominant explanatory factor are the MEMs components, with 12.3 % of the global variation (Fig. 6a). The intersection of the contribution of the environmental and MEMs components is 6.1% (Fig. 6a). The forward selection analysis assigned NDVI-season index and sand to Habitat and minimum temperature to Climate and discarded the other variables. Both Climate and Habitat have a small contribution when compared to the positive MEMs components (Fig. 6b), and only minimum temperature and the MEMs components had a significant partial contribution ($p < 0.05$, Fig. 6b). In summary, we find that positive MEMs representing positive temporal correlation explains a much larger significant contribution than environmental variables.

Species-specific abundance trends

Visually, *Erythrolamprus poecilogyrus, Philodryas patagogoniensis,* and *Xenodon dorbignyi* show a tendency of decreased abundance through time, while *Lygophis flavifrenatus* and *Helicops infrataeniatus* have a stable abundance (Fig 7). Overall, our GLMM models show that there is a tendency of abundance decrease in all species except *Helicops infrataeniatus* (Table 6). However, in *Erythrolamprus* the intercept is not significant and in *Lygophis flavifrenatus* and *Philodryas patagoniensis* the p-values of the periods and the intercept, respectively, are borderline. Furthermore, the R^2 values are very low in *L. flavifrenatus* and *P. patagoniensis* but very high in *Erythrolamprus*. Periods of time as fixed effects show important sources of variation at each time step. The random structure composed by month and season explains an important portion of the variance in the abundances of these snakes (R^2, Table 7). Additive random structures of month and season are predominant among these species, and an interaction structure of *season:month* is detected in *E. poecilogyrus*.

Support for our results comes from the model validation. We used the random structure to reduce the correlation between periods and generated a visual representation of the residuals and sample units (i.e., months, n = 92). The auto-correlation reduces with each sampled unit. In all species, the first year always shows autocorrelation, but it decreases rapidly with each time step (S3 Fig). At the same time, we validated the predictive potential of each fitted model. The observed zeros in our dataset are always within the predicted variation (S4 Fig).

Specific species Responses

Xenodon dorbigny. Grassland, Wind, and Seasons are important variables to explain abundance variation. Abundance increases during the spring and autumn decreased in summer (S2 Appendix, Fig 7). The Incidence Rate Ratios (IRT) increases with all significant variables.

Philodryas patagoniensis. Grassland and season are the variables that better explain the observed variation (S2 Appendix). The IRT is low when compared with *X. dorbingy.* Winter and sand predict the highest IRT, which can be interpretated as good predictive of abundances.

Erythrolamprus poecilogyrus. Sand is the only predictive variable. Although the sand IRT is the highest when compared to all other IRTs among species, the confident interval (CI) is also the broadest (S2 Appendix).

Helicops infrataeniatus**.** Only precipitation and temperature are potential predictors of abundance (S2 Appendix).

Lygophis flavifrenatus. Wind and temperature that represent climatic variables were selected, but just Temperature was significant, in the final model. Wind could not be removed from the final model. So that, temperature and wind are important variables to this species (S2 Appendix).

Discussion

Community and species-specific temporal dynamics

We detect important changes in several environmental variables in the study area between 1998 and 2021 (Fig. 3). These changes follow the trends reported for coastal dunes in Brazil [45] and worldwide [6]. Importantly, we detect an increase in the probability of reduction of community composition inferred from pairwise comparisons of periods (Fig. 4). We also show that when community composition is grouped according to the components of the temporal positive correlation (MMEs), the enviromental variables urbanization, grassland vegetation, wind, and temperature explain a linear effect ($R^2 = 0.41$, $p < 0.0001$). Despite these results, when we separated the effect of enviromental variables from those of MEMs on community composition, the environmental variables have a small effect when compared to that of the MEMs (Fig. 6).

The reduction of the snake community composition is accompanied by a negative abundance tendency of specific species, except for *Helicops infrataeniatus* (Table 6) that seems to have a stable tendency (Fig 7, Table 6). At the same time, we show that random structure composed by season and month represents an important source of individual variance within each period (Table 6), whereas the environmental model for each specific species reduces the random structure to the time periods. We interpret this result as indicative that the individual variance of each species at each time period combined with environmental variables are more important to explain abundance tendencies.

Explaining changes in community composition and population by environmental conditions is complicated because one needs long-term studies to make inference about populations and fine-scale environmental data [46]. Furthermore, spatial auto-correlation is a problem and analytical tools are need improving [47]. Thus, studies involving tropical and sub-tropical snake communities for comparisons with our results are limited. For example, within the *Pampa* biome, seasonal variation was described, with temperature considered a limiting factor whereas precipitation was uncorrelated with snake encounter rates [48]. The same study reported differential changes in abundance following a disturbance event caused by burning pasture, while one species (*Philodryas agassizii*) showed a decline in abundance, another increased it (*Erythrolamprus poecilogyrus*). A notable study in a Neotropical rainforest, documented a reduction of snake community composition and richness linked to the decrease of prey availability [28]. Mass mortality of amphibians—one of the most common prey items for snakes—caused by the infection with chytrid fungus *Batrachochytrium dendrobatidis* was accompanied by a general pattern of abundance decline in almost all snakes [28]. At community level, our data suggests that an increase of urban areas, and a decrease of grassland play a role in the observed changes in community composition. However, this effect is low when compared with the MEMs components, which explain a larger variance. Thus, we suggest that future studies should try to include both biotic interactions or at least indirect parameters, such as body condition as a proxy to variation in prey availability. This approach proved crucial to understand population dynamics in the snake *Bothrops insularis*. In this species, periods of food scarcity suggest a strong influence of climatic stochasticity and the dynamics of the movement of migratory birds [49]. In another example, males of tropical snake *Opheodrys aestivus* reduced body condition and population size also declined together with rainfall [50].

At population level, we detect a drop in abundance of *Xenodon dorbignyy* across periods. Whereas the environmental model indicates that summer has a negative effect on its abundance, the other variables show a positive relation (S2 Appendix). During

1998–2004, we recorded in the study area multiple egg-clutches of this species, which suggests that food availability is high [51]. During 2020–2021, we did not find egg-clutches of *X. dorbigngy* and more importantly, we did not record gravid females close to oviposition during the reproductive season in November–December [51]. For *Philodryas patagoniensis* and *Erythrolamprus poecilogyrus*, we also detected a negative tendency across periods, but this result must be taken with caution because the intercept and the slope were not statistically significant, respectively. The environmental model indicate a negative tendency by season in *P. patagoniensis*, but not in *E. poecilogyrus*.

Overall, these three species show a negative abundance tendency that accompanies a pattern of community composition reduction. However, the environmental variables that we used do not explain the negative pattern, except by reductions associated with summer in *X. dorbigngy* and all seasons in *P. patagoniensis*. This could indicate, as we saw at the community level, that environmental variables have a low power to explain changes of species abundance. For example, causes of the declines in snake populations of eight European species between 1990 and 2010 remain unknown, even though all of these species occur in areas subjected to increasing anthropogenic pressures [52]. In this study, five of the eight European species are characterized by small home ranges surrounded by urban areas. Furthermore, these five species have a preference for anurans as prey. This also mirrors our study system, where *P. patagoniensis*, although a trophic generalist, have a preference for anurans of the genus *Leptodactylus* [53] and *E. poecilogyrus and X. dorbignyi* are anuran specialists [54,55].

Statistical analysis approaches and inference limitations

Studying the responses of a community in a temporal scale framework possess serious analytical problems of auto-correlation measures and variance homogeneity (i.e., heterogeneity in the residuals). These are the most important assumptions of multivariate and univariate classical statistical techniques [4,5,37]. Because our data consists on repeated measures in the same local area, heterogeneity and auto-correlation becomes the norm. In an attempt to infer change in community composition while trying to diminish the impact of heterogeneity and auto-correlation, we used an community composition ordination analysis as suggested by [28]. This is a Bayesian approach recommended when sample size for most species is low, as it takes into account the variable and imperfect species detection [56]. However, a comparable sampling design is needed to avoid spurious results. For this reason, we used pairwise comparisons between periods with the same number of unit samples (*months* in our case), while checking that sample effort (i.e., number of days and accumulate minutes) are also comparable. In fact, we our sampling effort during periods 8 and 9 is larger than that of period 7 (Table 1). This is particularly important because there is a 15 years sampling gap between period 7 and 8. Thus, we can argue that the inferred high probability of reduction in community composition between periods 7 and 8 is not an artifact of sampling effort.

The 15 years sampling gap of our study opens an additional question. The probability of reduction of community composition inferred from our data during the first three years came to a halt in period 5 and remained until period 7 (Fig 4), with the reduction starting again when comparing period 8 with 7. Therefore, the inferred reductions could be cyclical, rather than linear. Unfortunately, our 15 years sampling gap does not allow to discern between these two scenarios. A complementary approach for future studies could investigate neutral process using simulations and test if ecological drift could better explain the ordination analysis and the percent of unknowledge variance inferred by us. Confronting neutral process and changing environmental conditions could be an interesting approach to overcome to partially mitigate the always limited amount of data when addressing community composition over time [57].

We studied specific species abundances by univariate methods and attempted to minimize autocorrelation using GLMM with random structure [58] [59]. However, despite the acceptable results of our model validation gave, incorporating random structure into GLMM does not directly model temporal correlation [58]. GAMM [60] is an alternative method to model it, but we cannot apply it because we have several nominal variables. Also, because we cannot incorporate imperfect detection in the GLMM, we could not studied the less abundant species. Perhaps hierarchical multi-species modelling [63] could allow for estimation of species-specific parameters (e.g., occurrence, abundance, and/or covariate effects) as well as community-level effects [64].

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Supporting information

All supplementary material is available for download from

https://brpucrs-my.sharepoint.com/:u:/g/personal/10084819_pucrs_br/EVhAjKvV2GVEvbXAZ_WOvLYBo380vNegQpCjYO_OSoNhrA?e=MVlN6g

S1 Table. Effort distribution across periods (1-9). Each row represents a survey into a month.

S2 Table. Complete data set of snake community abundance among Periods (1-9).

S1 Appendix. Supplementary material to extract environmental variables.

S2 Appendix. Estimated regression parameters from a Poisson GLMM of the habitat environmental model of the five most abundance species.

S1 Fig. Dissimilarity measure analysis

S2. Fig. Correlation degree between Bray-Curtis-NMDS

S3 Fig. Predictive potential of model base on abundance trends across periods.

S4 Fig. ACF plot base on abundance trends across periods.

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TABLES

Table 1. Sampling organized by periods of time, sampling units per period (i.e., months), and sampling effort in number of total days and accumulated minutes per period with searches, with mean and standard deviations (SD) for each period in parentheses.

Period	**Years**	**Samples**	**Days**	**Minutes**
1	98–99	11	74 (6.7 ± 3.07)	13985 (1271.36 ± 787.72)
2	99–00	12	88 (7.3 ± 3.11)	18605 (1550.42 ± 908.61)
3	00–01	12	88 (7.3 ± 2.99)	26130 (2177.5 ± 1347.55)
4	00–02	12	80 (6.7 ± 3.5)	23075 (1922.92 ± 962.63)
5	02–03	12	111 (9.3 ± 2.18)	28135 (2344.58 ± 1044.86)
6	03–04	12	74 (6.2 ± 1.53)	11150 (929.17 ± 371.37)
7	04	7	28 (4.0 ± 1.53)	5301 (757.29 ± 373.03)
	05–19		Sampling Gap	
8	20–21	7	33 (4.7 ± 2.63)	9050 (1292.86 ± 724.29)
9	21	7	36 (5.1 ± 1.57)	9667 (1381 ± 825.85)
Total	9	92	612	145098

Table 2. Original 14 environmental variables used to characterized the study area. For each year, we coded season by month (in parentheses). Source refers to raster layer except for Tramandai meteorological station.

Variable	Units	Source, spatial resolution
Evapotranspiration	kg m^{-2} s^{-1}	NASA/FLDAS/NOAH01/C/GL/M/V001, 11132 m
Soil moisture	kg/m2	
Soil temperature	K	
Near surface air temperature	K	
wind speed	m s^{-1}	
Precipitation	mm/day	[UCSB-CHG/CHIRPS/DAILY], 5000 m [Landsat 5, 7, 8], 30 m
Sand	ha	
Urban	ha	
Grassland	ha	
Pinus	ha	
Normalized Difference Vegetation Index	[0.1–1]	
Minimum temperature	C°	WorldClim, ~21 km2 (98–04) | Tramandai Automatic Station (20–21), ~21 km
Maximum temperature	C°	
Season	Qualitative	Spring [9, 10, 11], Summer (12, 1, 2), Autumn (3, 4, 5), Winter (6, 7, 8)

Table 3. Snake species found at the sampling area ordered by decreasing number of encounters (N). Average number and standard deviation (SD) of encounters per sampling period is in parentheses when N > 10.

Species	**N**	**Mean**	**SD**
Xenodon dorbignyi	622	38.88	36.24
Philodryas patagoniensis	507	31.69	18.66
Erythrolamprus poecilogyru	312	19.50	13.17
Helicops infrataeniatus	153	10.20	8.19
Lygophis flavifrenatus	115	7.67	3.33
Erythrolamprus jaegeri	59	4.54	3.53
Erythrolamprus semiaureus	59	4.54	3.67
Bothrops alternatus	21	2.10	1.52
Boiruna maculata	6	-	-
Phalotris lemniscatus	5	-	-
Taeniophallus poecilopogon	3	-	-
Oxyrhopus rhombifer	2	-	-
Thamnodynastes sp	2	-	-
Philodryas aestiva	1	-	-

Table 4. Selected environmental predictors, their variance inflation factor (VIF), and correlated variables according to pairwise Pearson's correlations.

Environmental predictors	**Nomenclature**	**Correlated variables**	**VIF**
Evapotranspiration	evap_tavg	Soil temperature [0.74]	3.46
NDVI by season	ndvi_Season	Pinus [0.80], Sand [-0.67]	1.66
Urban	Urban	Sand[-0.93], Pinus [0.85]	2.17
Precipitation	precip	Soil tempeture [0.87]	2.89
Minimum temperature	tmin	Near surface air temperature [0.98], Maximum temperature [0.97], soil temperature [0.99]	1.98
Grassland	Grassland	Low positive [0.0-0.18] and negative [0.05-0.5] correlation with all variables	1.57
Wind	wind_f_tavg	Low negative correlation with all variables [0.04-0.18]	1.13

Table 5. The nine significant MEMs related to variation in snake community composition ordered by their decreasing statistical significant as determined by the p-value.

Variable	R^2	R^2 adjust	F	p-value
MEM9	0.055	4%	5.286	0.000
MEM11	0.103	8%	4.724	0.000
MEM10	0.130	10%	2.684	0.013
MEM16	0.154	11%	2.493	0.021
MEM30	0.178	13%	2.491	0.024
MEM5	0.223	16%	2.425	0.024
MEM2	0.245	17%	2.396	0.026
MEM27	0.200	14%	2.413	0.030
MEM1	0.264	18%	2.173	0.049

Table 6. Results of a fixed effects GLMM model on the abundance of five snake species. The intercept is an offset variable *(log (Number of days))*, and the R^2 represent a pseudo-r obtained by bootstraps. D is the dispersion of residuals in the model, and Cor is the correlation between the Intercept and Period.

Species	Fixed effect	Estimate	Std. error	z value	Pr(>|z|)	R^2	D	Cor
Xenodon dorbignyi	(Intercept)	-5.12926	0.258	-19.909	0.000*	19.89%	1.10	0.557
	Periods	-0.10873	0.034	-3.166	0.002*			
Philodryas patagoniensis	(Intercept)	0.11231	0.166	0.676	0.499*	5.09%	1.13	0.862
	Periods	-0.07792	0.034	-2.284	0.022*			
Lygophis flavifrenatus	(Intercept)	-1.5579	0.243	-6.400	0.000*	0.33%	1.59	
	Periods	-0.03335	0.049	-0.677	0.498*			
Erythrolamprus poecilogyrus	(Intercept)	-0.09373	0.126	-0.745	0.456	52.75%	1.22	0.776
	Periods	-0.15438	0.027	-5.646	0.000*			
Helicops infrataeniatus	(Intercept)	-2.32709	0.480	-4.844	0.000*	0.71%	1.75	0.486
	Periods	0.05932	0.051	1.160	0.246			

* $p < 0.05$

Table 7. Results of a random effects GLMM on the abundance of five snake species. The intercept is an offset variable *(log (Number of days))*, and the R^2 represent a pseudo-r obtained by bootstraps. The intercept *season:month* represent the interaction between these variables.

Species	Random effect (Groups)	Variance	Std.Dev.	R^2
	Intercep			
Xenodon dorbignyi	month	0.1087	0.3298	40.02%
	season	0.1045	0.3233	
Philodryas patagoniensis	month	0.00332	0.0576	5.56%
Lygophis flavifrenatus	month	0.04266	0.2065	2.43%
Erythrolamprus poecilogyrus	season:month	0.0336	0.1833	57.15%
Helicops infrataeniatus	month	1.645	1.283	56.77%

FIGURES

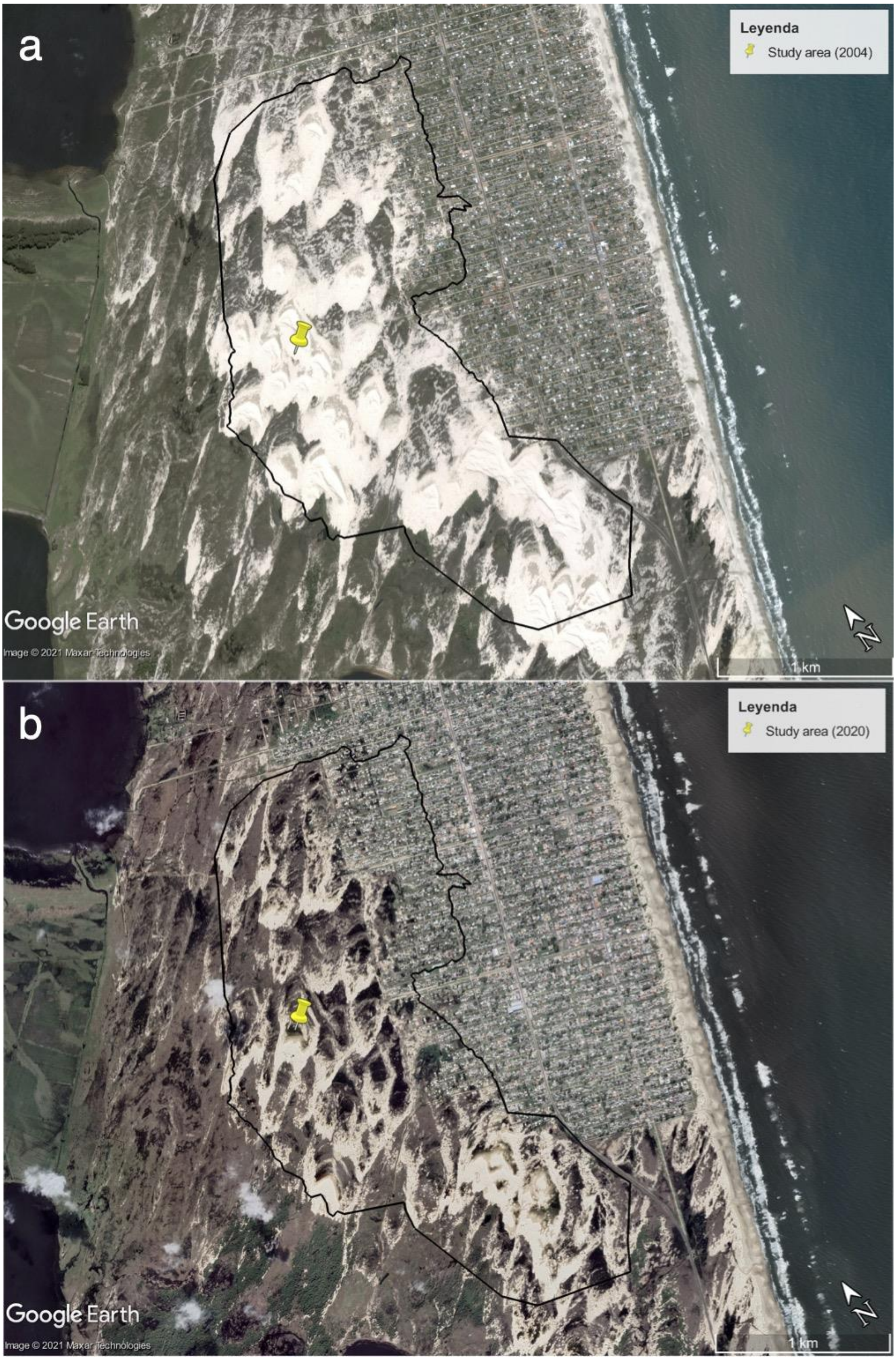

Fig 1. Study area. Comparative images Landsat of 2004 and 2020.

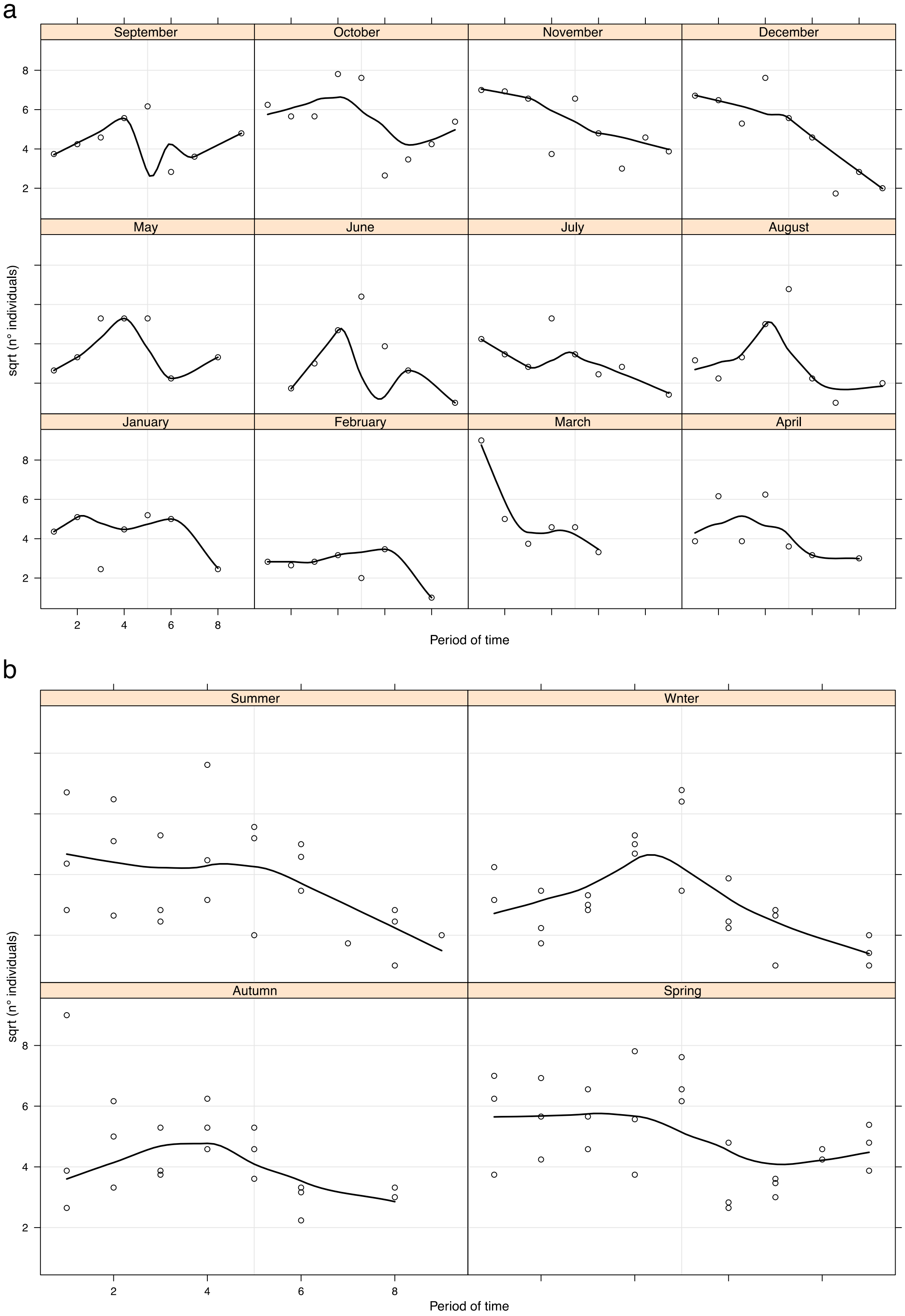

Fig 2. Variation of snake community abundance between periods (1–9) by month (A) and season (B). All graphs have the same scale values.

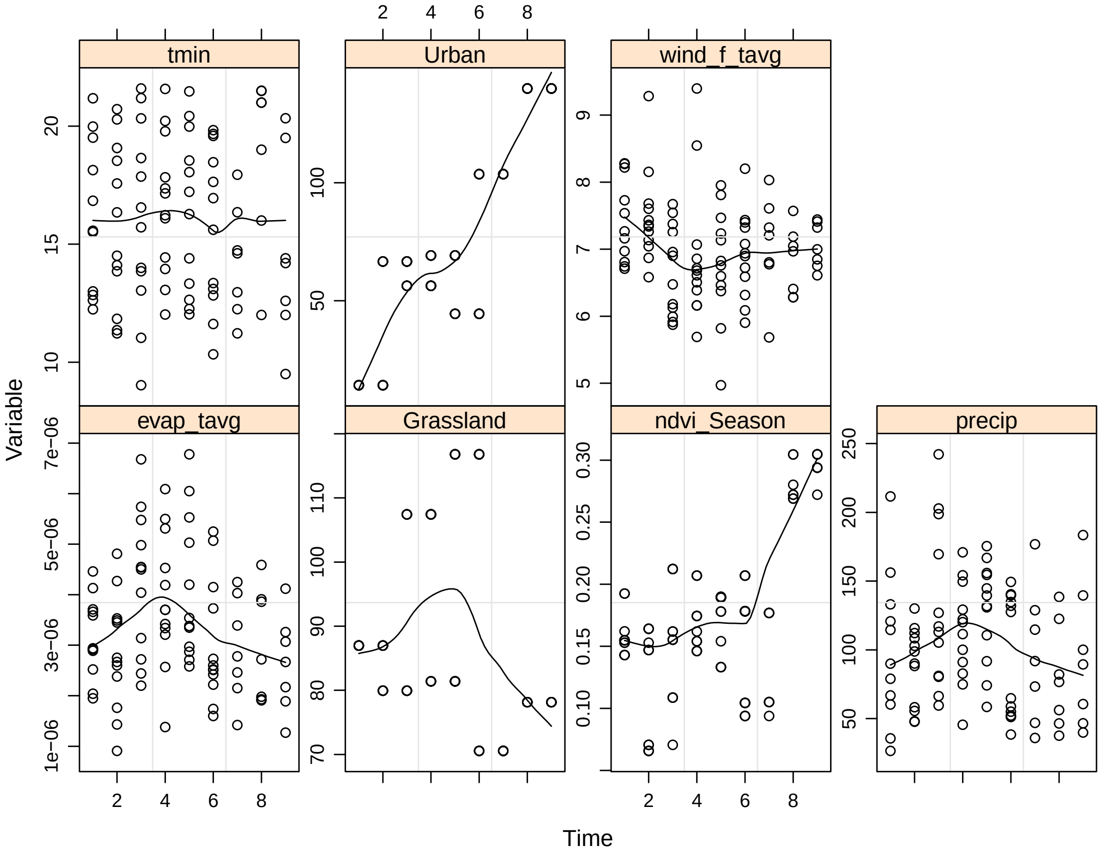

Figure 3. Variation of environmental variables through periods of time. See Table 4 for information on variables. All graphs have the same scale values in the time axis.

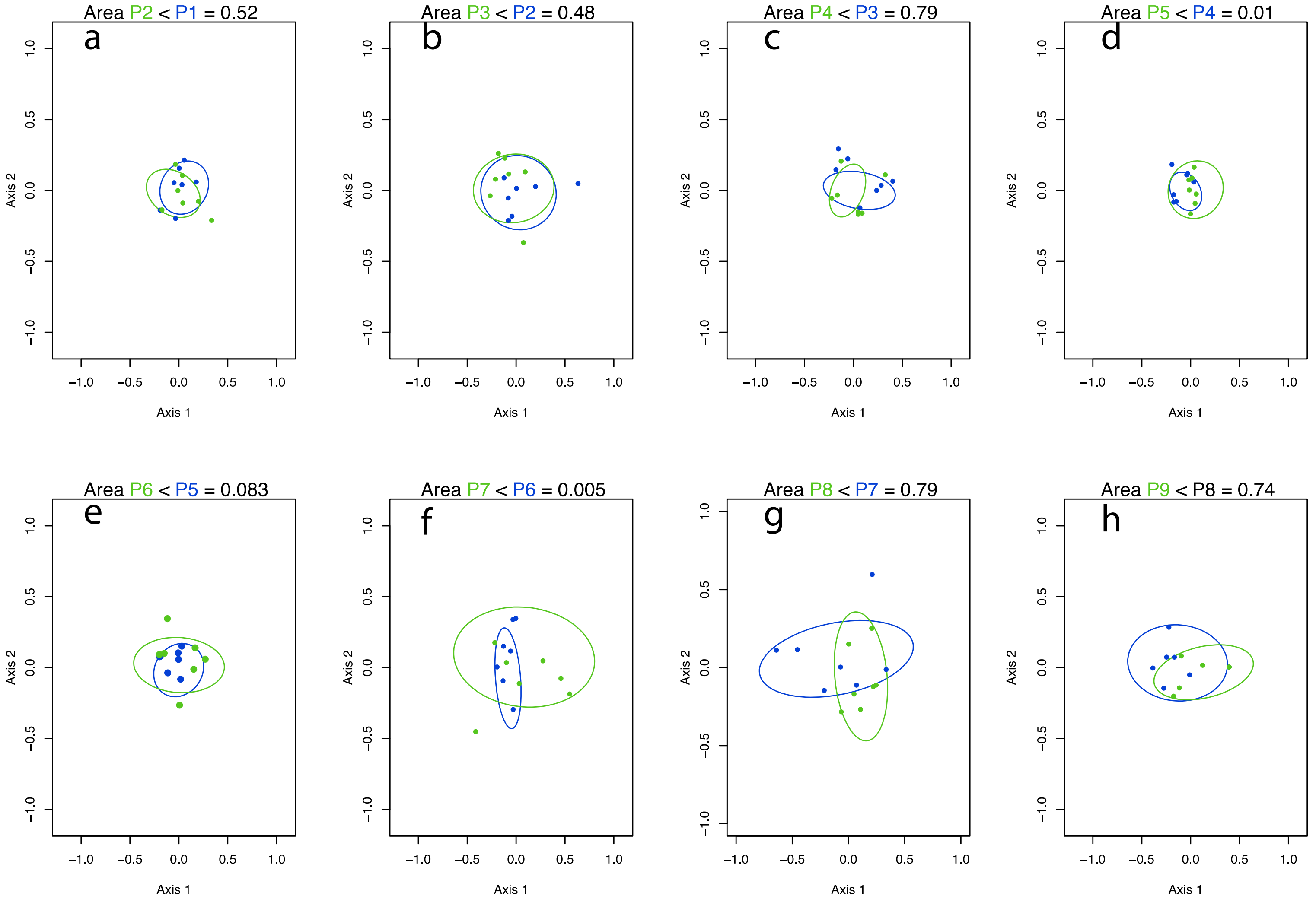

Fig 4. Probability of decrease in snake community composition across time periods (1–9).

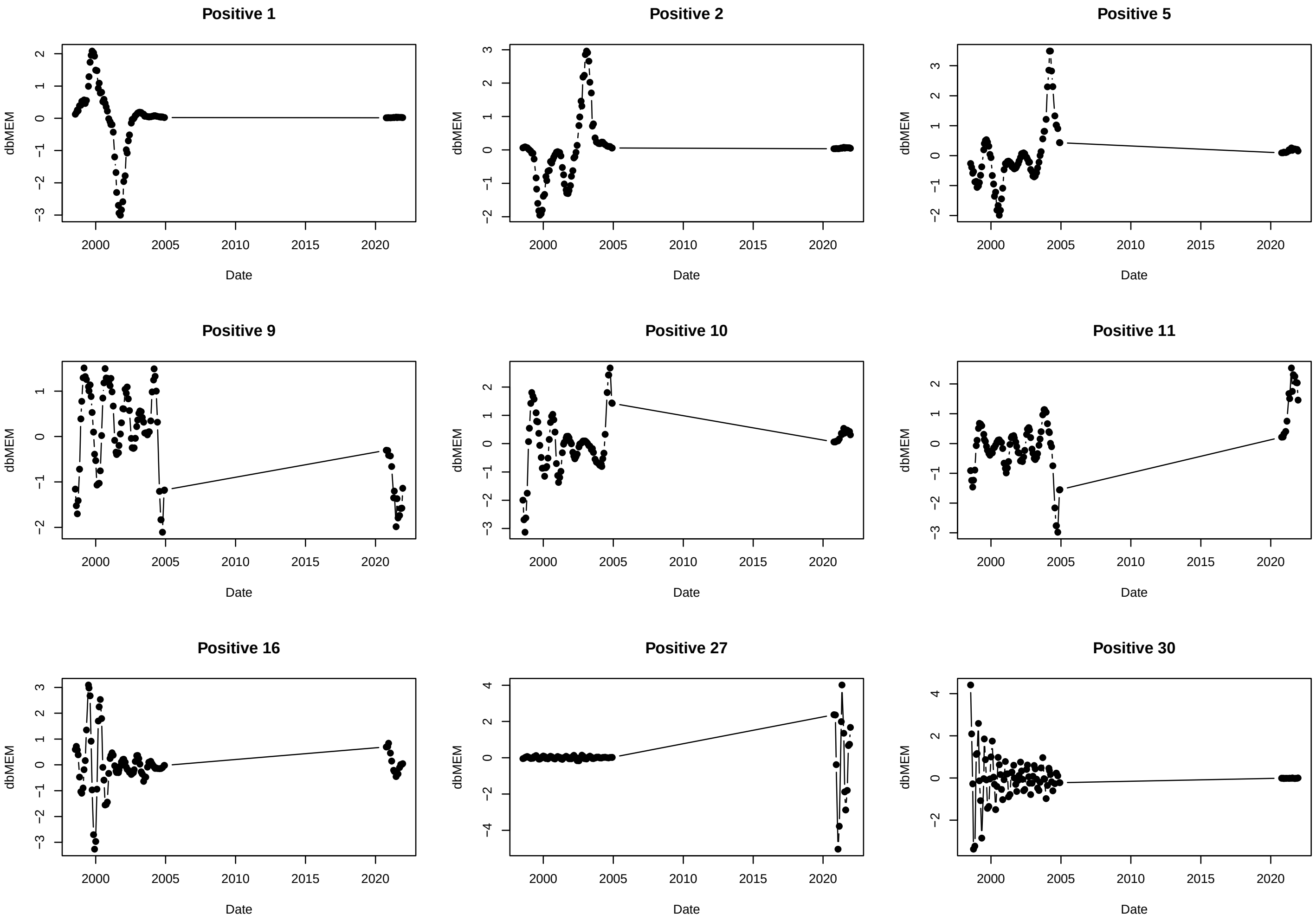

Fig 5. Variation across time of statistically significant positive MEMs.

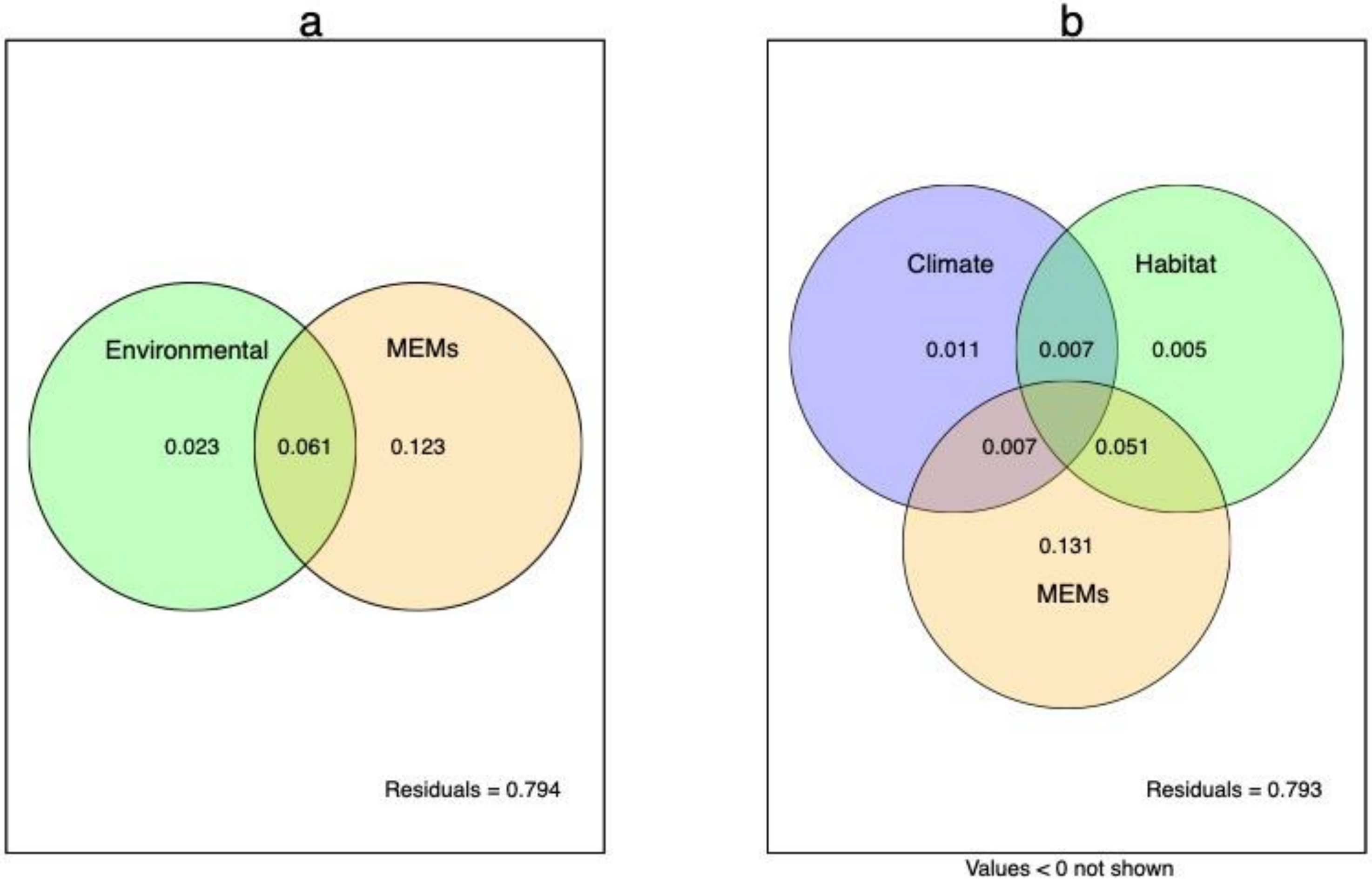

Fig 6. Relative variation on snake community of different variables. (a) MEMs and environmental variables and (b) MEMs and Climate and Habitat variables. See main text for composition of each class of variables.

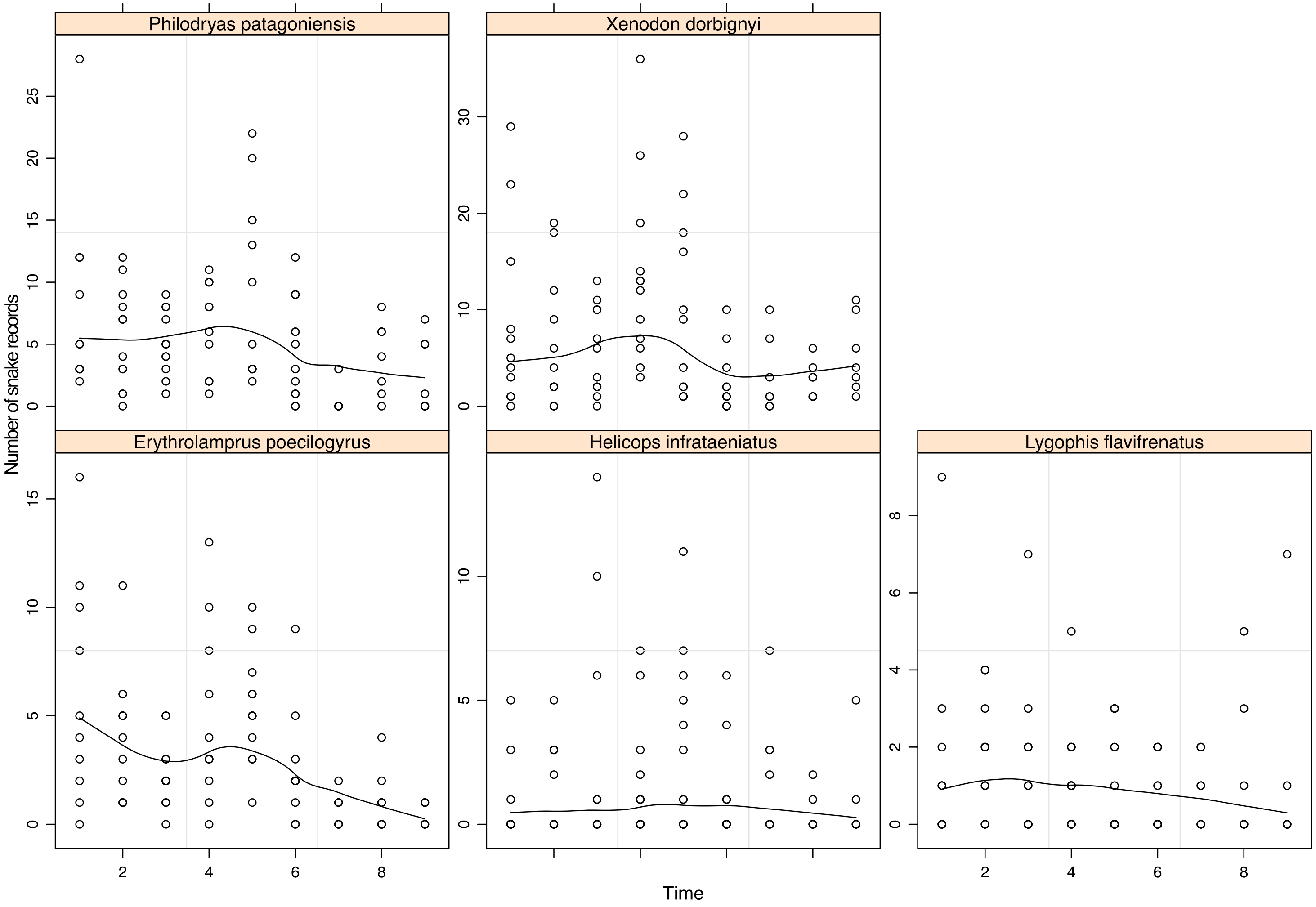

Fig 7. Snake species abundance across nine periods of time.