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Influence of environmental variables on the spatiotemporal distribution of anurans during the reproductive season in south-eastern Brazil

Influencia de variables ambientales en la distribución espacio-temporal de anuros durante la época reproductiva en el sureste de Brasil

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ABSTRACT. The Southeast region of Brazil contains a great wealth of species of anuran amphibians, which face several threats, such as environmental degradation and climate change. Therefore, it is necessary to carry out more studies on the influence of environmental variables on their space-time distribution, especially in the breeding season. The objective of the study was to identify the main climatic and habitat variables that influence the distribution of anuran amphibians in Serra do Japi, São Paulo, Brazil. Data collection in the field was carried out on a fine scale, at the study sites Montanhas do Japi (MJ) and Sítio do Sol (SS), where the

environmental variables: climatic (temperature and relative humidity of the air) and terrain elevation were measured, as well as the habitat variables (types of substrate, position within the substrate, terrain slope, height of the individual to the ground, and distance to the water mirror). The variables elevation, temperature and relative humidity were analyzed using Pearson's correlation coefficient; while habitat and location variables were evaluated through a multivariate approach, using cluster analysis with the k-means technique. In MJ, four groups were obtained, with six species of frogs, where the predominant one was *Brachycephalus rotenbergae*. In SS, three groups were obtained, with seven species, where the predominant one was *Phyllomedusa burmeisteri*. Spatiotemporal distribution was obtained under a different combination of variables, where fine information was included on substrate (water or adjacent to water, soil, vegetation) and position of the observed individual (in water or soil, leaf litter, herbaceous/shrub vegetation). It was confirmed that there is an environmental climate dependence on the reproductive conditions of anurans living in Mata Atlântica conditions, although there is little variability explained based on the analyzed data. These results contribute to the generation of more specific knowledge about the requirements of frogs during their breeding season.

Key words: Atlantic Forest; cluster analysis; direct development amphibians; indirect development amphibians; k-means

RESUMEN. El sureste de Brasil contiene una gran riqueza específica de anfibios anuros, los cuales enfrentan diversas amenazas, tales como degradación del ambiente y el cambio climático. Ante esto, es necesario realizar más estudios sobre la influencia de las variables ambientales en su distribución espacio-temporal, especialmente en la época reproductiva. Por ello, el objetivo de este estudio fue identificar las principales variables ambientales, climáticas y del hábitat, que influyen en la distribución de anfibios anuros en la Serra do Japi, São Paulo, Brasil. La toma de datos en campo se realizó a escala fina, en los sitios de estudio Montanhas do Japi (MJ) y Sítio do Sol (SS), donde se midieron variables ambientales: climáticas (temperatura y humedad relativa del aire) y elevación del terreno, así como variables del hábitat (tipos de sustrato, posición dentro del sustrato, pendiente del terreno, altura del individuo al suelo y distancia al espejo de agua). Las variables elevación, temperatura y humedad relativa fueron analizadas a través del coeficiente de correlación de Pearson; mientras que las variables del hábitat y ubicación se evaluaron mediante un enfoque multivariado, utilizando análisis de cluster con la técnica de k-medias. En MJ se obtuvieron cuatro cluster, con seis especies de anuros, donde la predominante fue *Brachycephalus rotenbergae*. En SS se obtuvieron tres cluster, con siete especies, donde la predominante fue *Phyllomedusa burmeisteri*. Se obtuvo la distribución espacio temporal bajo diferente combinación de variables, donde se incluyó información fina sobre el sustrato (agua o adyacente al agua, suelo, vegetación) y la posición del individuo observado (en el agua o sobre el suelo, hojarasca, vegetación herbácea/arbustiva). Se confirmó que hay dependencia de situaciones ambientales y climática en las condiciones reproductivas de los anuros que viven en condiciones de Mata Atlântica, aunque hubo poca variabilidad explicada con base a los datos analizados. Estos resultados contribuyen en la generación de conocimiento más puntual sobre los requerimientos de los anuros durante su época reproductiva.

Palabras clave: análisis cluster; anfibios de desarrollo directo; anfibios de desarrollo indirecto; k-medias; Mata Atlântica

INTRODUCTION

Anurans represent more than 85% of all amphibian species (Frost, 2023) and play an important role in terrestrial and aquatic ecosystem services (Hocking & Babbitt, 2014; Springborn *et al.*, 2022). They inhabit a wide variety of habitats and microhabitats depending on their biological characteristics and evolutionary history, such as reproductive mode, life cycle, skin permeability, and low dispersal capacity, but are particularly dependent on environmental variables, like climatic and habitat vegetation (Covarrubias *et al.*, 2021; Nunes-de-Almeida *et al.*, 2021). Additionally, the structure and complexity of the vegetation, together with the availability of water and meteorological conditions, provide favorable microhabitats for feeding, refuge, and oviposition sites, positively related to the richness and abundance of anuran species (Ferreira *et al.*, 2016; Figueiredo *et al.*, 2019; Pereira *et al.*, 2020; Tavares-Junior *et al.*, 2020). Directly developing species lay their eggs in cavities in the ground or in trees, under trunks or leaf litter, and in vegetation (leaves and bromeliads). As the development of the individuals takes place inside the egg, these species need high levels of environmental humidity to avoid desiccation. On the other hand, the species of indirect development need temporary or permanent bodies of water for the development of their aquatic larvae, for which they deposit their eggs in the water, in the submerged vegetation or in the one that protrudes from the water (Haddad & Prado, 2005; Nunes-de-Almeida *et al.*, 2021).

Related to the above, it is worth mentioning that deforestation and climate change alter the structure of the landscape, with a negative impact on ecosystems and biodiversity (Prevedello *et al.*, 2019; Weiskopf *et al.*, 2020; Meyer *et al.*, 2022), and raise the level of threat of anuran populations (Covarrubias *et al.*, 2021; Lambertini *et al.*, 2021). Habitat fragmentation caused by deforestation reduces the availability of oviposition sites and protection sites for eggs, juveniles, and adults against predators, both for species with direct and indirect development (Ferreira *et al.*, 2016; Covarrubias *et al.*, 2021; de la Sancha *et al.*, 2021). In addition to this, the decrease in plant cover and the edge effect allows greater sunlight to enter the fragment, increasing evapotranspiration levels, reducing environmental humidity (Prevedello *et al.*, 2019), increasing the risk of desiccation of eggs and juveniles of species of direct development (Covarrubias *et al.*, 2021), and limiting the oviposition sites (Ferreira *et al.*, 2016).

Climate change alters the rainfall regime, increases droughts, and affects the oceanic air masses that bring moisture to the interior of the continent (Santos *et al.*, 2020; Meyer *et al.*, 2022), reducing the availability of water bodies that serve as breeding grounds for species with indirect development, as well as the survival of aquatic larvae (Brannelly *et al.*, 2019). Furthermore, the increase in temperature also favours the spread of pathogens such as the fungus *Batrachochytrium dendrobatidis* Longcore, Pessier & Nichols (Bd), which has caused a decline in amphibian populations worldwide in recent years (Lambertini *et al.*, 2021; Sopniewski *et al.*, 2022).

Given the transformation of ecosystems caused by deforestation and climate change, coupled with the potential threat of the Bd fungus, it is essential to fill the knowledge gaps on climate and vegetation variables that influence the spatiotemporal distribution of anurans. These transformations produce effects on biodiversity at different spatial scales (Weiskopf *et al.*, 2020). In the case of anuran amphibians, it is necessary to change the spatial resolution to a finer one when it comes to analyzing individuals with limited movement capacity, in addition to considering their biological requirements, and highly specialized and diverse reproductive modes (Vasconcelos *et al.*, 2010; Figueiredo *et al.*, 2019; van der Hoek *et al.*, 2019).

The Serra do Japi, located in south-eastern Brazil, has a high diversity of anuran amphibians (Fundação Serra do Japi, 2008; van der Hoek *et al.*, 2019; Nunes *et al.*, 2021). However, its natural conditions have been affected by deforestation due to urban expansion and the threat of climate change and emerging pathogens (Fundação Serra do Japi, 2008; Ballerini *et al.*, 2021; Carrasco *et al.*, 2021). For this reason, the survival of this diversity of species is now at greater risk (Ballerini *et al.*, 2021), which is why studies focused on the conditions present on a fine scale are necessary. Based on the above, the objective of this research was to identify the main environmental (climatic and habitat) variables that influence the spatiotemporal distribution of anuran amphibians during the reproductive season in Serra do Japi, São Paulo, Brazil.

MATERIALS AND METHODS

Study area. The Serra do Japi, Guaxinduva e Jaguacoara, due to its landscape condition and extraordinary biodiversity, was declared a Reserva da Biosfera da Mata Atlântica in 1992 by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Currently, it houses one of the last continuums of native vegetation in the state of São Paulo (Escobar *et al.*, 2017). It is located in the southeast region of the state of São Paulo and is delimited by an irregular polygon (Fig. 1), with extreme coordinates UTM 7432.00-7414.00 N and 307.00-286.00 E, in the municipalities of Jundiaí, Cabreúva, Pirapora do Bom Jesus and Cajamar (Condephaat, 2020).
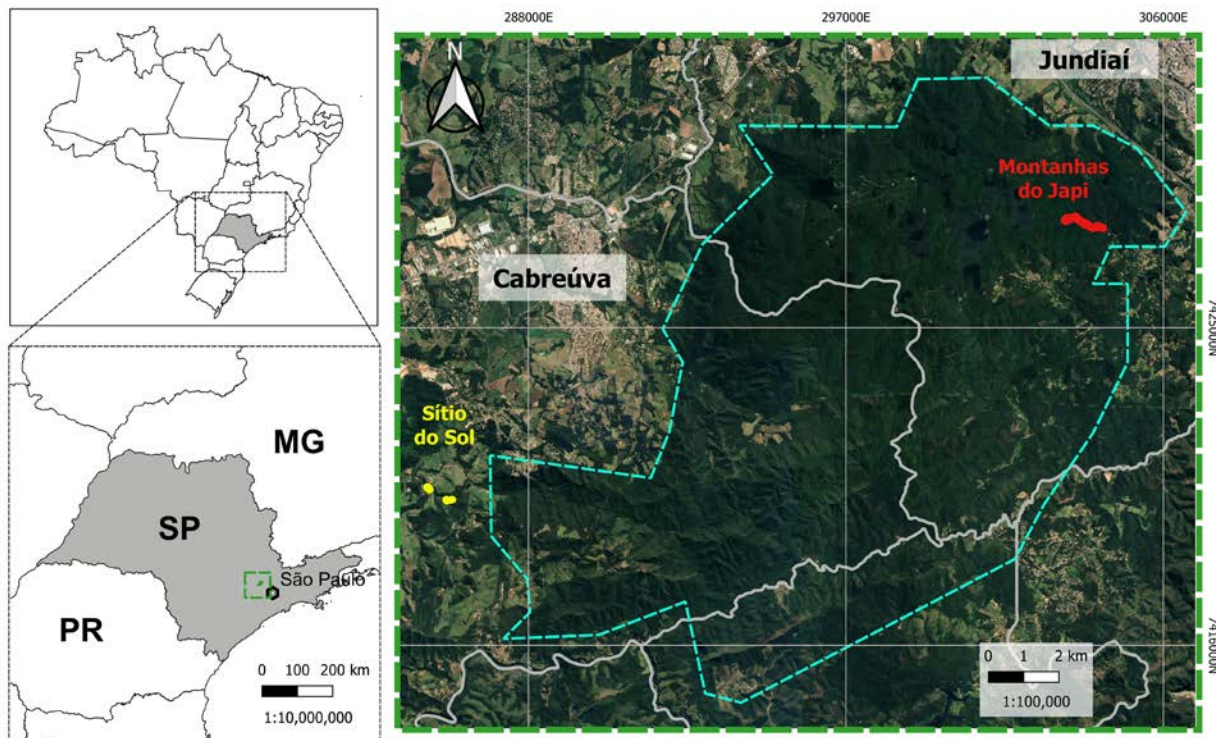
Figure 1. Location of sampling sites for anuran amphibians during the reproductive season in Serra do Japi, south-eastern Brazil. The turquoise dotted polygon represents the area proposed by Condephaat (2020). Brazilian states acronyms are: MG = Minas Gerais; SP = São Paulo; and PR = Paraná.

This area is home to important springs, streams, and rivers, as well as particular geological features. The topography is rugged, with an elevation between 660 and 1200 m above sea level (masl). The predominant climates in Serra do Japi are Cfa and Cfb, according to the Köppen-Geiger climate classification, with rainy summers (December-March) and dry winters (June-September).

The vegetation, for the most part, is made up of secondary vegetation where the semi-deciduous seasonal forest predominates. It is worth mentioning that Serra do Japi is located in an ecotonal region of the Mata Atlântica and Cerrado biomes (Hasui *et al.*, 1978; Ab'Sáber, 2003; Cardoso-Leite *et al.*, 2005; Escobar *et al.*, 2017). Although the present study did not consider vegetation type as a variable, it should be mentioned that representative plant species for Mata Atlântica are *Ormosia minor* Vog. (endemic), *Bathysa meridionalis* L.B.Sm. & Downs, *Croton floribundus* Spreng, *Guapira opposita* (Vell.) Reitz, and *Maytenus salicifolia* Reissek, whereas for Cerrado are *Callisthene minor* Mart (endemic) and *Trichilia pallida* (SW) (Fundação Serra do Japi, 2008).

The present study was carried out in two sampling sites located in different portions of the Serra do Japi. The first site, Montanhas do Japi is located in the municipality of Jundiaí, while the second site, Sítio do Sol, is in the municipality of Cabreúva (Fig. 1). It is worth mentioning that only the first sampling site was located within the polygon proposed by the Conselho de Defesa do Patrimônio Histórico, Arqueológico, Artístico e Turístico do Estado de São Paulo (Condephaat, 2020).

Montanhas do Japi (MJ). The work was carried out within the Fazenda São Francisco das Montanhas farm, with 329 ha, on a path 2.6 km long, approximately 2 m wide (Fig. S1 A), mainly under closed canopy, with few sections with open canopy, crossing small streams. This trail was built and is used for environmental education tours, with an elevation range from 790 m to 1030 masl. It is important to note that the adjacent areas were well preserved (Fundação Serra do Japi, 2008).

Sítio do Sol (SS). This part of the work was carried out at the IJAPI - Instituto Japi de Pesquisas, Ações Ambientais e Desenvolvimento Humano, based on a property called Sítio do Sol – Cultura Indígena. It consists of 27 ha, with an elevation of 655 to 705 masl, where most of its vegetation cover is made up of secondary vegetation. Three observation sites were considered, with an approximate area of 5800 m^2 (Fig. S1 B). The first site corresponded to an artificial pond of approximately 2200 m^2 and its surroundings composed of bare soil, gravel, sand, and herbaceous vegetation. The second was in a temporary stream, with an extension of around 900 m^2 and a dense arboreal and shrubby vegetation on both banks. The third, with an area of approximately 800 m^2, centered on a lake with an estimated surface area of 220 m^2 and completely covered by floating vegetation of the genus *Lemna*. Around 50% of its periphery was covered by *Hedychium coronarium* J. Koenig (white ginger), and the rest was covered by arboreal and shrubby vegetation (Fundação Serra do Japi, 2008).

Field sampling. Records of anuran occurrence and the measurement of several variables of the sampling sites were taken from September to December 2021, corresponding to the rainy season and reproductive season of anurans. The sampling effort for both sites was eight random days, not necessarily consecutive. In MJ, sampling was exclusively during the day, from 8:30 to 18:30 h, due to access restrictions to the farm and to the conditions of accessibility, space, and habits of the main anuran species, although nocturnal species also inhabit this site. To adjust to the conditions of each site with respect to the duration of each sampling session, these were adjusted to 2.5 h (D1: 8:30:00–11:00; D2: 11:00–13:30; D3: 13:30–16:00; D4: 16:00–18:30). In SS, the sampling was nocturnal, from 19:00 to 23:00 h, due to the exclusively nocturnal habits of the species that are distributed there. In this site, the sampling data were divided into one-hour sessions (N1: 19:00–20:00; N2: 20:00–21:00; N3: 21:00–22:00; N4: 22:00–23:00).

At both sampling sites, an active search (sound and visual) was carried out for the individuals to locate and record the occurrence of anuran amphibians. The electronic identification guide Anfíbios da Mata Atlântica (Toledo *et al.*, 2021) was used for the correct taxonomic

identification of the individuals. For each record, along with the location and identification, the sighting time (ST) and geographic coordinates (GC) were taken using Garmin satellite geoprocessing equipment (GPS), model GPSMap 64SX, datum WGS84. In addition, for each occurrence record, precise information on climatic, elevation, and other habitat variables were registered.

The climatic variables (CV) were: (Temp) = temperature (°C) and (RAH) = relative air humidity (%), both obtained using an Elitech brand data logger, model RC-61, which was turned on during the entire journey in each sampling session, taking records every 30 s, and at the point of each anuran occurrence. Because of its close relationship with the previous variables, (TE) = terrain elevation (masl) was also registered using a GPS Map 64SX, datum WGS84. The habitat variables (HV) were: (TS) = terrain slope (°), obtained with the Laser Level and Inclinometer smartphone application (Version 1.5.02, EXA Tools, 2020), and others related to the substrate and position when observed. The type of substrate (Sub) was classified into three categories: (1) water or adjacent to water, (2) soil, and (3) vegetation. In turn, the position of the individual when observed (PIO) was classified according to each type of substrate. For substrate (1), the categories were: a) partially submerged at the water's edge, b) totally submerged, c) white ginger vegetation, and d) herbaceous vegetation. For substrate (2), the categories were: a) bare dry on slight slope, b) bare dry on steep slope, c) bare wet, d) bare gravel/stone on slight slope, e) bare gravel/stone on steep slope, f) plant litter on a slight slope, and g) plant litter on a steep slope. For the substrate (3), the categories were: a) herbaceous, b) shrubby - leaves, c) shrubby - branches, d) shrubby - trunk, e) arboreal - branches, and f) arboreal - trunk. Both the (DWM) = distance (m) to the water mirror and the (HIGr) = height (m) of the individual in relation to the ground were considered, obtained with a Mileseey laser tape measure, model X5. The distance of the individuals to the mirror of the water was classified in intervals of 0.50 m, starting at 0 m and ending at > 10 m, generating 21 ranges in total.

Both the GPS and the data logger were programmed to automatically take measurements every 30 seconds. Upon initiation of the active search for anurans, both sets were turned on at the same time to obtain all TE, Temp, and RAH data for the duration of each sampling session. Subsequently, the information obtained with the GPS was concatenated with the information obtained with the data logger.

Data processing. Data collected with GPS was downloaded using Garmin BaseMapTM software and exported as a file format for use in Excel (Windows 10). The data collected with the data logger was downloaded through the ElitechLog software and exported for later use in the same Excel software. All the information was concatenated, adding GC, TE, Temp and RAH data, generating the CV database for each sampling site. The information from the anuran occurrence records was also transcribed into an Excel spreadsheet, generating the HV database for each sampling site, with precise information on each observed individual: species, ST, GC, TE, Temp, RAH, Sub, PIO, TS, HIGr and DWM. Finally, the information was reviewed, deleting duplicate, incomplete or incorrect data.

Statistical analyses. Statistical analyses were performed using the SigmaPlot for Windows software version 10.0 (Systat©, 2006) and RStudio version 4.1.1 (RStudio©, 2009). The data were analyzed descriptively, considering the minimum and maximum values, as well as the mean and its respective standard deviation (SD). For the CV variables per site, the Pearson correlation coefficient (Elith *et al.*, 2006) was used to determine the association between TE and the Temp and RAH variables.

The HV data were evaluated using a multivariate approach, specifically cluster analysis (hclust:stats), where it was sought to generate groupings from the variables: TE, Temp, RAH, ST, Sub, PIO, TS, HIGr and DWM, in those cases that had occurrence records of anuran species. The optimal number of clusters was identified using the function fviz_nbclust:factoextra for each of the study sites (Fig. S2), determining that it was necessary to work with four groups in MJ (k = 4) and with three groups in SS (k = 3). Two dendrograms (Fig. S3 A and B) were made using the *hclust* function (*ward.D2* and euclidean distance methods). Derived from the previous groups, it was decided to apply the k-means technique to group the data (Ahmed *et al.*, 2020).

RESULTS

The CV and TE influenced the spatiotemporal distribution of anurans. In MJ's case, the TE values ranged from 795.6 to 986.9 m, with a mean of 899.6 m ± 39.54 S.D. The minimum and maximum Temp were 16.4 and 37.5 °C, respectively, with a mean of 21.4 °C ± 3.10 S.D. The RAH fluctuated between 50.9 to 100%, with a mean 88.9% ± 10.28 S.D. In the case of SS, TE ranged from 655.1 to 705 m, with a mean of 681.5 m ± 8.25 S.D., Temp was 17.4 to 26.10 °C, with a mean of 20.4 °C ± 1.37 S.D., and RAH was from 68.4 to 100%, with a mean of 89.3% ± 6.20 S.D.
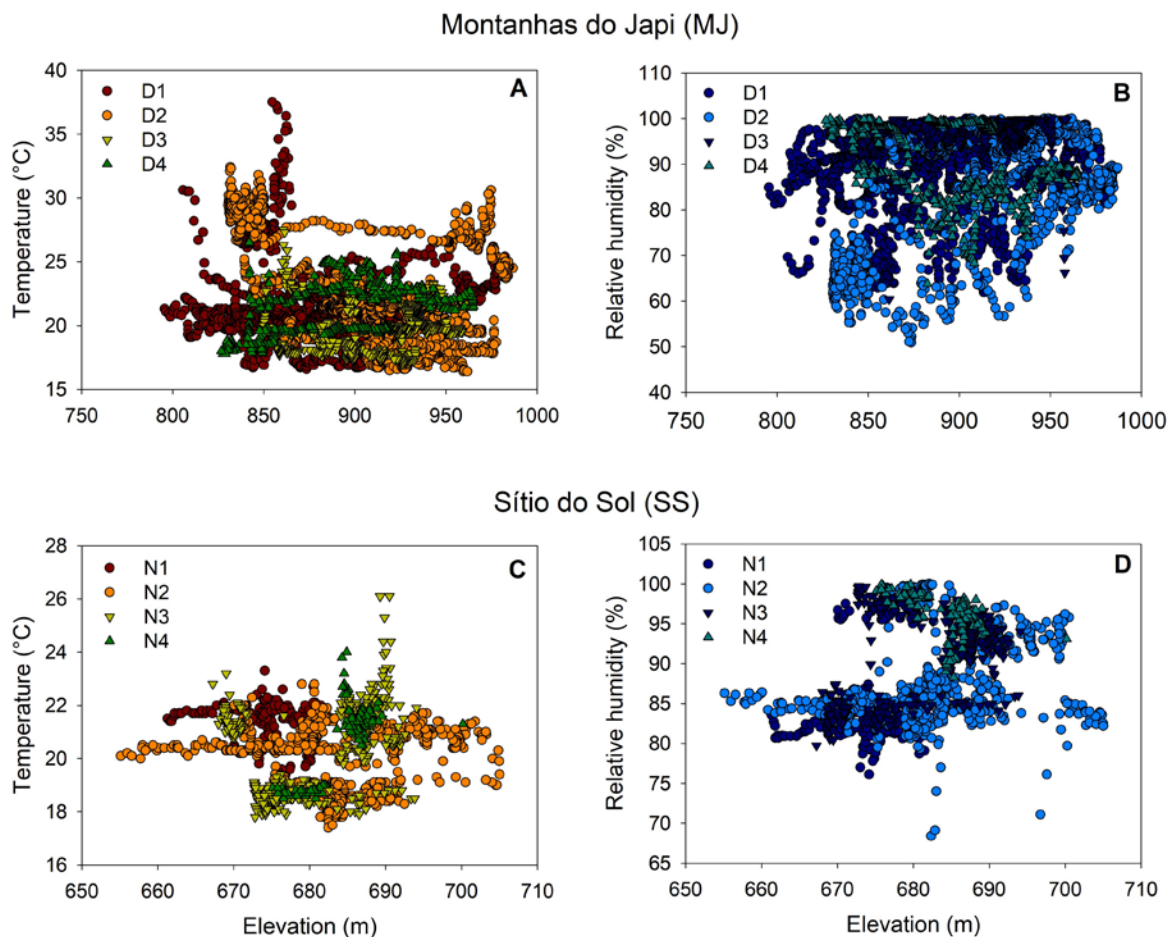
**Figure 2.** Dispersion of temperature (A and C) and relative humidity (B and D) data along the elevation gradient at the Montanhas do Japi (A and B) and Sítio do Sol (C and D) sampling sites, São Paulo, Brazil.

The Temp and RAH data at both sites did not present a distribution pattern along TE (Fig. 2). For the MJ site, based on Pearson's correlation analysis, there was a negative association (*r* = -

0.20) between Temp and TE, while the correlation between RAH and TE (r = 0.28) was positive. For the SS site, both Temp (r = 0.02) and RAH (r = 0.30) showed a positive correlation with TE.

Cluster analysis. The k-means analysis explained 49.4% of the variability of the MJ data set (Fig. 3). Cluster 1 included 82 records, with two species of anuran amphibians (*Brachycephalus rotenbergae* Nunes, Guimarães, Moura, Pedrozo, Moroti, Castro, Stuginski, and Muscat: n = 71, and *Ischnocnema* sp.: n = 5) of direct development (92.7%), and two species (*Procerathrophys boiei* (Wied-Neuwied)): n = 3 and juveniles of *Rhinella* sp.: n = 3) of indirect development (7.3%). For this cluster, there was an elevation range of 836.3 to 945.5 masl, with a mean of 898.3 masl; the temperature fluctuated from 20.3 to 24.3 °C, with a mean of 21.9 °C; and the relative humidity of the air oscillated between 72.7 to 97.3%, with a mean of 89.4%. The observations of the individuals occurred more frequently between 11:00 h and 13:30 h (40.2%) and at a distance greater than 10 m from the water mirror (31.7%). For these observations, the predominant type of Sub and PIO were soil with plant litter on a steep slope (58.5%). In this cluster, the slope of the terrain fluctuated from 1 to 85°, and the height of the individual from the ground from 0.01 to 0.91 m.
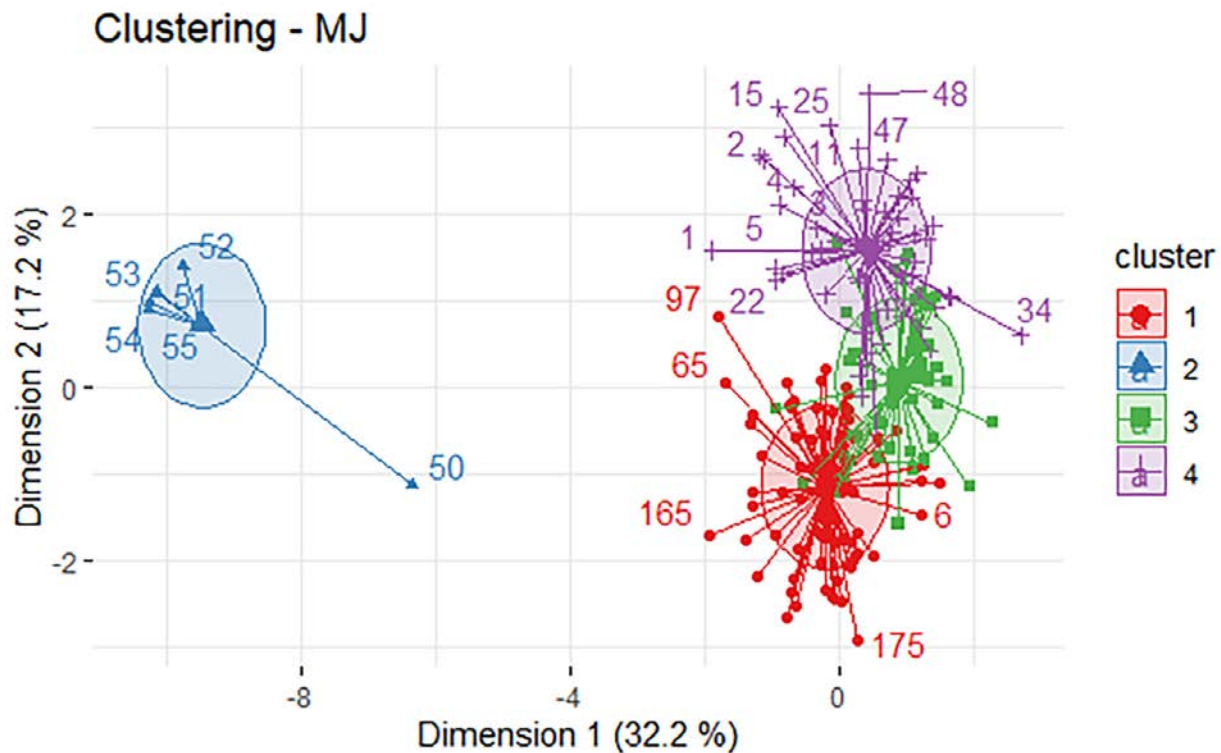
Figure 3. Cluster k-means for standardized data of six species of anuran amphibians, during the breeding season in Montanhas do Japi (MJ), based on climatic variables (land elevation, temperature and relative humidity of the air), and habitat (type of substrate, the position of the individual when observed, distance to the water mirror, slope of the land, and height of the individual to the ground). In addition, the time of registration was considered. The first cluster included 82 records, the second six, the third 60, and the fourth 54 records. The conditions for clusters 1, 3 and 4 were more similar to each other with respect to cluster 2, which differed from the previous ones.

Cluster 2 included six records with one species (*B. rotenbergae*: n = 5) of direct development (83.3%) and one (*Bokermannohyla luctuosa* (Pombal and Haddad): n = 1) of indirect development (16.7%). The TE range was 838.2 to 845.2 m, with a mean of 842.0 m; Temp fluctuated from 26.3 to 28.3 °C, with a mean of 26.9 °C; and RAH was from 67.1 to 74.4%, with a mean of 69.1%. The

observations of the individuals occurred mainly between 8:30 and 11:00 h (83.3%), with DWM between 0.51 and 1 m (83.3%), and the predominant Sub and PIO were water or adjacent to water with herbaceous vegetation. (83.3%). In this cluster, TS fluctuated from 31 to 47° and HIGr was 0.01 m.

Cluster 3 included 60 records, with one species (*B. rotenbergae*: *n* = 58) of direct development (96.7%) and two species (*Rhinella ornata* (Spix): *n* = 1 and juvenile *Rhinella* sp.: *n* = 1) of indirect development (3.3%). The range of TE was 878.4 to 975.1 m, with a mean of 926.4 m; Temp fluctuated from 18.8 to 24.1 °C, with a mean of 20.5 °C; and RAH was from 82.5 to 100%, with a mean of 95.8%. The observations of the individuals occurred mainly between 11:00 and 13:30 h (45.0%), with DWM greater than 10 m (28.3%). For these observations, the predominant Sub and PIO were soil with plant litter and other remains of trees on a steep slope (65.0%). In this cluster, TS fluctuated from 0 to 58° and HIGr from 0.01 to 0.27 m.

Cluster 4 included 54 records, with two species (*B. rotenbergae*: *n* = 48 and *Ischnocnema* sp.: *n* = 5) of direct development (98.1%) and one species (juvenile of *Rhinella* sp.: *n* = 1) of indirect development (1.9%). The TE range was 831.9 to 953.3 m, with a mean of 897.7 m; Temp fluctuated from 14.4 to 25.0 °C, with a mean of 19.0 °C; and RAH was from 89.2 to 99.7%, with a mean of 95.51%. The observations of the individuals occurred mainly between 8:30 h and 11:00 h (46.3%), with DWM greater than 10 m (18.5%). For these observations, predominant Sub and PIO were soil with plant litter on scarce and steep slopes (81.5%). In this cluster, TS fluctuated from 1 to 69° and HIGr from 0 to 0.69 m.
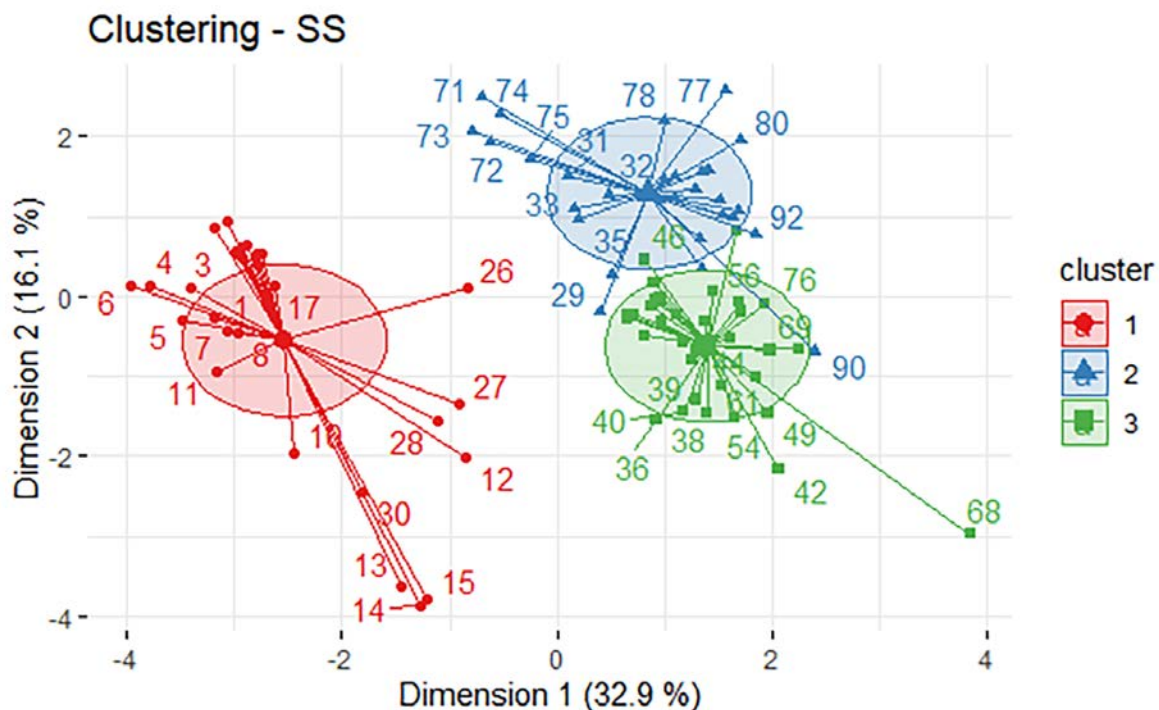
Figure 4. Cluster k-means for standardized data of seven species of anuran amphibians during the reproductive season in Sítio do Sol (SS), based on climatic variables (land elevation, temperature and relative humidity), and habitat (type of substrate and the position of the individual when observed, distance to the water mirror, slope of the land and height of the individual to the ground). In addition, the time of registration was considered. The first cluster included 29 records, the second 29, and the third 35 records. The conditions for clusters 1 and 3 were more similar to each other with respect to cluster 2, which differed from the previous ones.

For the SS data set, the k-means analyses explained 49.0% of the variability (Fig. 4). Cluster 1 included 29 records, with six species of anuran amphibians of indirect development (*Boana prasina* (Burmeister)): *n* = 4, *Leptodactylus latrans* (Steffen): *n* = 1, *Phyllomedusa burmeisteri* Boulenger: *n* = 4, *Rhinella ornata*: *n* = 2, *Rhinella icterica* (Spix): *n* = 17 and *Scinax fuscovarius* (Lutz): *n* = 1). The TE range was 668.4 to 687.8 m, with a mean of 676.4 m; Temp fluctuated from 17.2 to 20.5 °C, with a mean of 19.0 °C; and RAH was from 81.9 to 100%, with a mean of 95.8%. The observations of the individuals occurred mainly between 19:00 and 20:00 h (51.7%), with DWM values of 0 m (44.8%). For these observations, the predominant Sub and PIO were in the water or adjacent to the partially submerged water at the shore (44.8%). In this cluster, TS fluctuated from 0 to 78° and HIGr from 0 to 1.12 m.

Cluster 2 included 29 records, with three species of indirect development (*Boana faber* (Wied-Neuwied)): *n* = 8, *P. burmeisteri*: *n* = 16, and *R. icterica*: *n* = 5). The TE range was 667.2 to 682.7 m, with a mean of 677.0 m; Temp fluctuated from 18.5 to 23.6 °C, with a mean of 21.7 °C; and RAH was from 71.1 to 86.9%, with a mean of 81.86%. The observations occurred mainly between 20:00 and 21:00 h (41.4%), and DWM values fluctuated between 0 and 0.5 m (55.2%). For these observations, the predominant Sub and PIO were water or adjacent to water in the *H. coronarium* vegetation (44.8%). In this cluster, TS was from 2 to 43° and HIGr from 0 to 1.31 m.

Cluster 3 included 35 records, with two species of indirect development (*L. latrans*: *n* = 1 and *P. burmeisteri*: *n* = 34). The range of TE was 674.4 to 699.3 m, with a mean of 686.4 m; Temp fluctuated from 19.7 to 23.9 °C, with a mean of 21.5 °C; and RAH was from 80.8 to 96.6%, with a mean of 91.6%. The observation of the individuals occurred mainly between 21:00 and 22:00 h (45.7%), with DWM between 0.51 and 1 m (31.4%). For these observations, the predominant Sub and PIO were water or adjacent to water in the *H. coronarium* vegetation (48.6%). In this cluster, TS was from 2 to 16° and HIGr from 0 to 3.38 m.

DISCUSSION

Climatic variables have a direct influence on the distribution of anuran amphibian species. For example, temperature has an influence for terrestrial species of direct development, but it is secondary to the habitat's humidity (Polettini Neto, 2013; Nunes *et al.*, 2021). In fact, the variables related to environmental humidity are key factors in the richness and composition of anuran communities, especially for those of indirect development, which can present various reproductive modes, some of which are very specialized (Vasconcelos *et al.*, 2010; Silva *et al.*, 2012). In the study, the results for the RAH and Temp variables showed adequate values for the reproductive conditions of anurans, in accordance with Silva *et al.* (2012) and Nunes *et al.* (2021). It is worth mentioning that, although the sampling areas in each of the sites were relatively small, there were subtle changes in climatic conditions. Thus, although weak, there was a correlation between Temp and TE, and between RAH and TE in Montanhas do Japi. In the first case, there was a negative correlation, which meant that Temp decreased as TE increased; while, in the second case, the correlation was positive; that is, RAH increased as TE increased. For Sítio do Sol, there was a weak positive correlation between Temp and TE, and between RAH and TE. However, at neither site was a clear pattern observed. For MJ, there was a TE gradient of 134.2 m, while for SS it was 32.0 m. These fluctuations in the variables influenced the groupings created with the cluster analysis, considering both the CV and HV variables.

In the case of Montanhas do Japi, it is worth mentioning that the combination of all types of Sub with leaf litter (PIO) was predominant, regardless of the slope of the terrain (TS), which also influenced the clusters. In this site, we found four groups of anuran amphibians, both of direct and

indirect development. The predominant species at this site, *B. rotenbergae*, is diurnal (Nunes *et al.*, 2021); however, *B. luctuosa*, *P. boiei* and the genus *Rhinella* are nocturnal (Frost, 2023). This set of species shared characteristics among them, depending on the variables involved, such as the time of day. Each cluster included a varying number of records, the largest (82) being in cluster 1, while cluster 2 included only six records. Regarding the species involved, there were four in cluster 1, two in cluster 2, three species in clusters 3 and 4; but these species were not exclusive to a single cluster, but some were repeated in two or more. Another relevant aspect for grouping were the characteristics of the anuran species based on their initial form of development (direct or indirect), as well as their life habits and degree of specialization, according to Nunes-de-Almeida *et al.* (2021).

Based on the foregoing, it is understandable to find *B. rotenbergae* in different groupings, since it is a species that lives and reproduces in leaf litter in humid cloud forest soils (Nunes *et al.*, 2021). Plant litter was the predominant PIO in clusters 1, 3 and 4. In cluster 2, which was the most differentiated from all the clusters, the predominant Sub and PIO were water or adjacent to water in herbaceous vegetation and, although *B. rotenbergae* remained the predominant species, this may be explained because this cluster registered the lowest values of RAH for all MJ. The other species present in this last cluster was *B. luctuosa*, which is arboreal, of the Hylidae Family and of indirect development, because the Sub and PIO conditions were adequate for this species, along with the lowest TE, the highest mean Temp, and the lowest DMW, which coincides with Frost (2023).

Besides the Sub, PIO and DWM conditions, the separation among the remaining three clusters was considered on Temp, RAH, TE, TS and HIGr conditions. Cluster 1 presented the highest amplitude of RAH and TS, the highest value of HIGr, and the lowest value of amplitude of Temp. In this cluster, *Ischnocnema* sp., *P. boiei* and *Rhinella* sp. (juvenile) were present in addition to *B. rotenbergae*. The species *Ischnocnema* sp. is also of direct development and reproduces in the moist soil, below the plant litter (Canedo & Haddad, 2012; Frost, 2023), which in addition to the present RAH and Temp were adequate for their reproductive success (Nunes-de-Almeida *et al.*, 2021; Frost, 2023). For their part, *P. boiei* and *Rhinella* sp. are of indirect development, which is why they require bodies of water for their oviposition sites (Ferrante, 2019; Preuss *et al.*, 2021; Frost, 2023). In addition, *Rhinella* sp. is very flexible in terms of the type of Sub and PIO (Preuss *et al.*, 2021), so it shared the same characteristics as the two species of direct development. For its part, *P. boiei* is cryptozoic, so it depends on nooks or fissures in the substrate where it can hide during daylight hours (Ferrante, 2019), but it also adjusted to the conditions of this cluster.

Cluster 3 presented the highest mean of TE, the highest recorded value of RAH, the lowest mean values and amplitude of HIGr, the lowest amplitude of TS and the lowest dispersion of DWM. Besides *B. rotenbergae*, it also included *Rhinella ornata* and *Rhinella* sp. (juvenile). It should be taken into account that the species of the genus *Rhinella* reproduce in the water, but their juveniles are terrestrial (Frost, 2023). Finally, cluster 4, except for *P. boiei*, included the same species as cluster 1. The peculiarity is that it presented the highest TE and Temp amplitude, and the highest Temp and RAH means.

For Sítio do Sol, the sampling was carried out in an extension similar to that of MJ, but with different conditions: there was a lower TE gradient, with a final elevation below the initial one in MJ, and with a lower mean TS. In this site, there was greater diversity, with seven species, and only *Rhinella ornata* was also present in MJ. It is worth mentioning that all these species developed indirectly and were nocturnal, and that the sampling was more focused on bodies of water and their surroundings. The presence records were more related to Sub in the water and PIO in

emergent vegetation, but also in Sub of vegetation and shrub PIO in branches. The latter is partly because half of the species found here (*B. prasina*, *B. faber*, *P. burmeisteri* and *S. fuscovarius*) are arboreal, which is also related to higher HIGr than in MJ. The rest of the species found in this site (*L. latrans*, *R. icterica* and *R. ornate*) are terrestrial (Frost, 2023), so there were other types of Sub and PIO registered. It is important to emphasize that these species share characteristics based on their reproductive mode, which depend on water, not only humid environments (Nunes-de-Almeida *et al.*, 2021).

Accordingly, for SS we found three groupings of anurans, in which six species participated in cluster 1, three in cluster 2, and two in cluster 3. Each set of species shared characteristics among them, in a different way, depending on both of climatic and habitat variables, such as the time of day. There was also a varying number of records, the largest (34) being in cluster 3, while clusters 2 and 3 included 29 records each. It is worth mentioning that *P. burmeisteri* was the only species in common in the three clusters, but it was not the most predominant. Thus, the explanation of the conditions that were grouped in each cluster is as follows.

Cluster 1 was the one that separated the most from the other two. In this cluster, the lowest values for mean, recorded value and amplitude of Temp were recorded, as well as the highest value for mean and recorded value of RAH, the lowest amplitude of HIGr, and the highest amplitude, mean and recorded value of TS. The species included were the arboreal *B. prasina*, *P. burmeisteri* and *S. fuscovarius*, and the terrestrial *L. latrans*, *R. icterica* and *R. ornata*. The most predominant species was *R. icterica*, recorded in the water or adjacent to it, which influenced this cluster to differ from the others by PIO, in addition to climatic conditions.

Cluster 2 comprised the highest values for the mean and amplitude of Temp, the lowest mean of TE, the lowest values for the mean and recorded value of RAH and HIGr predominantly between 0.0 – 0.5 m. This cluster included two arboreal species *P. burmeisteri* and *B. faber*, and one terrestrial *R. icterica*. The most dominant species was *P. burmeisteri* and the main PIO was white ginger vegetation. The subtle climatic fluctuations were what differentiated this cluster 2 from 3. On the other hand, cluster 3 included the largest number of records (n = 35), with the fewest number of species, where *P. burmeisteri* was markedly predominant. While the predominant Sub and PIO were the same as cluster 2, the differences were due to HIGr between 0.51 – 1 m, higher mean values and amplitude of TE, lower mean and amplitude of TS, and higher mean and amplitude of RAH.

Although directly and indirectly developing anuran species may have very different climatic and habitat requirements (Figueiredo *et al.*, 2019; Ceron *et al.*, 2020; Bertoluci *et al.*, 2021), they can also coexist spatially (Leão-Pires *et al.*, 2018; Pereira *et al.*, 2020). This was made clear in this work through cluster analyses. The different combination of species between the two study sites and the respective clusters were related to the various combinations of CV, HV, and time of day. It is worth mentioning that the different types of vegetation cover increase the availability of microhabitats that serve as shelter, food, and breeding sites for anurans, which directly influences their spatiotemporal distribution (Tavares-Junior *et al.*, 2020; McCallum & Trauth, 2021). In this sense, the study area presented different types of this cover, which together with the presence of water bodies (*e.g.*, Nunes-de-Almeida *et al.*, 2021), was reflected in the diversity of anuran species documented in this work. However, the low occurrence of individuals of some of the species could be attributed to the sampling time, especially in MJ, although the scarcity and delay of rain during the study period could also have had an influence (INMET, 2023).

There were some particular observations of some species regarding the occurrence of individuals in SS. In the pond, individuals of *R. icterica* and *R. ornata* were observed mainly in the

water or on the shore, while *S. fuscovarius* and *L. latrans* were observed in the surroundings of the pond, corroborating previous findings (Ferreira *et al.*, 2016; Figueiredo *et al.*, 2019; Pereira *et al.*, 2020). These same authors also point out the tolerance and adaptability of these species to modified environments, as was the case of this site. In the temporary stream, *B. prasina* specimens were perched on emergent vegetation. In the lake, the records of *P. burmeisteri* occurred mostly in the predominant vegetation (*H. coronarium*), followed by branches and bushes, while the specimens of *B. faber* were observed on the banks using the same vegetation, close to the ground. The distribution of species in different types of substrates and vegetation structure was reported by Pereira *et al.* (2020). Relatedly, Ferreira *et al.* (2016) mention that habitat use by anurans is mainly related to their reproductive modes.

It was considered that the conditions were propitious for the abundance of *P. burmeisteri*, based on its reproductive mode (specialist), since oviposition occurs on broad leaves of the vegetation around the water mirror (Andrade *et al.*, 2018; Nunes-de-Almeida *et al.*, 2021), which were present in our study site. It was also considered that the abundance of *R. icterica* was due to its basic biology and reproductive mode. This species is terrestrial and generalist, since it is usually observed even in urban environments, and although it requires bodies of water for oviposition, it uses them regardless of where they are (Haddad & Prado, 2005; Nunes-de-Almeida *et al.*, 2021; Oliveira-Souza *et al.*, 2022).

Regarding the objective of this study, it was confirmed that there is climatic dependency depending on the suitability of the habitat for the reproductive conditions of the registered species, coinciding with Haddad & Prado (2005); Nunes-de-Almeida *et al.* (2021) and Oliveira-Souza *et al.* (2022). Therefore, it is concluded that this objective was partially met, this due to the little variability explained by the data sets analyzed. However, it is necessary to emphasize that in this study, in addition to conventional climate and habitat variables, there were also other finer-scale considerations. In this regard, few investigations have analyzed the reproductive habitat of anurans at this scale (*e.g.*, Polettini Neto, 2013). The results of this study were reinforced with the participation of other very subtle variables, such as the substrate (Sub) and the position of the observed individual (PIO), both very specific to the specific site where each individual was recorded. Thus, the results presented were referred to very particular circumstances. One inconvenience, in this case, is that the rainy season was delayed, which could have affected these results. For this reason, it is recommended that the study period be extended in future research.

With this information, results of the spatiotemporal distribution were obtained, where different species of anuran amphibians were grouped under a different combination of variables through a series of clusters in each of the study sites. These results contributed to the generation of knowledge about the conditions required by the species of this taxonomic group the reproductive season, for this especially biodiverse region. However, a more detailed in exploration of the relevance of the variables used here, or others not considered, could help to better explain the variation in future investigations of this type.

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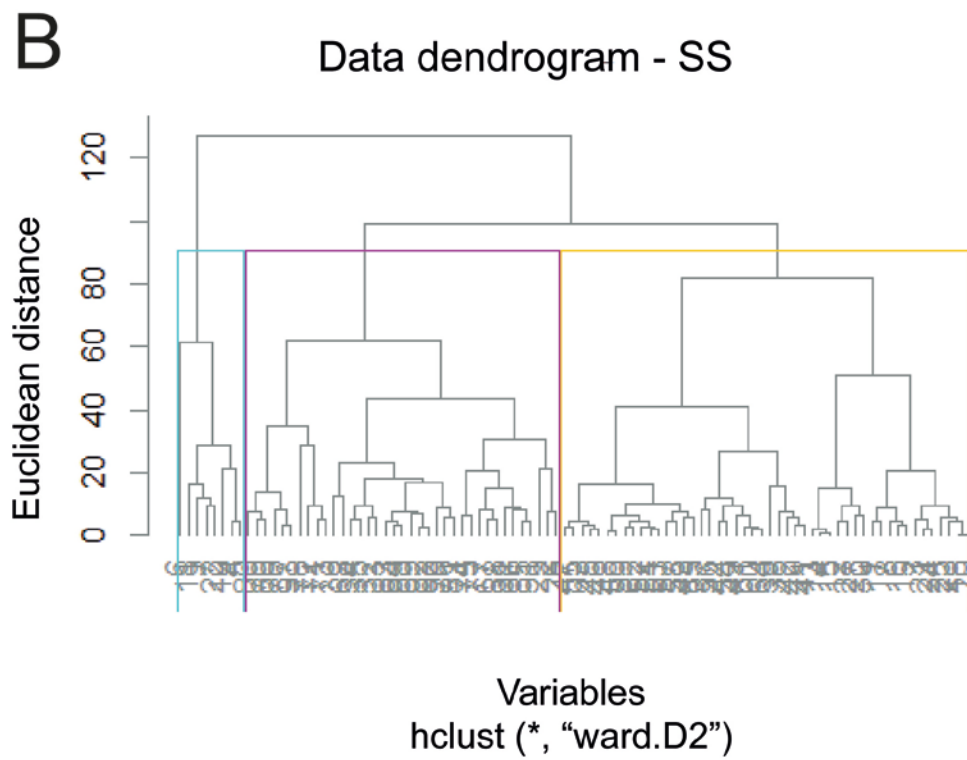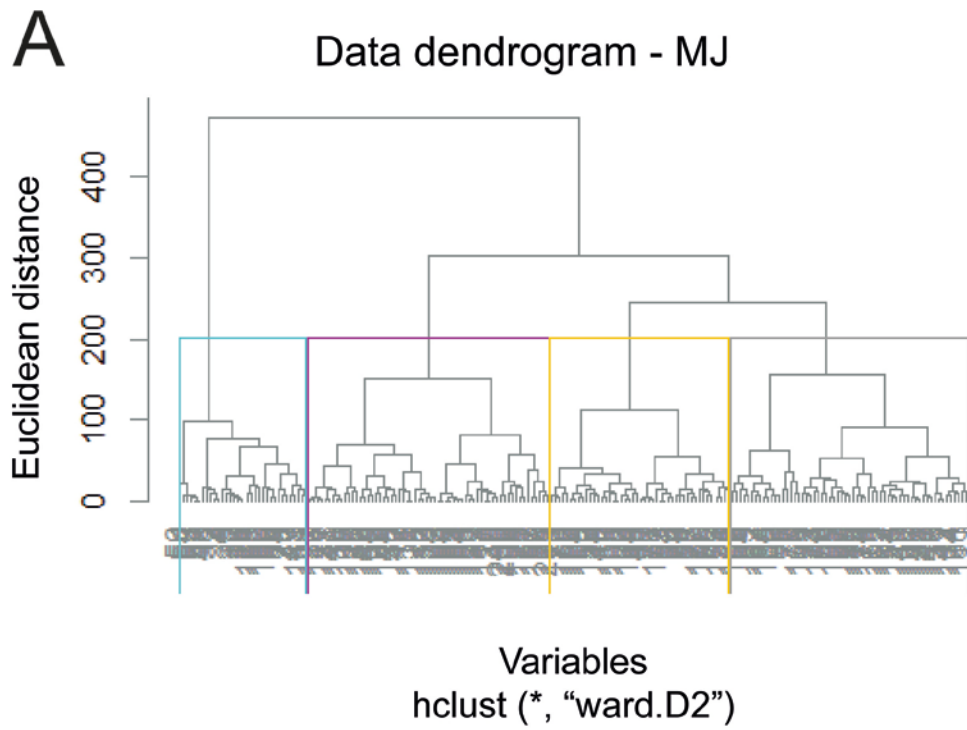
ANEXOS
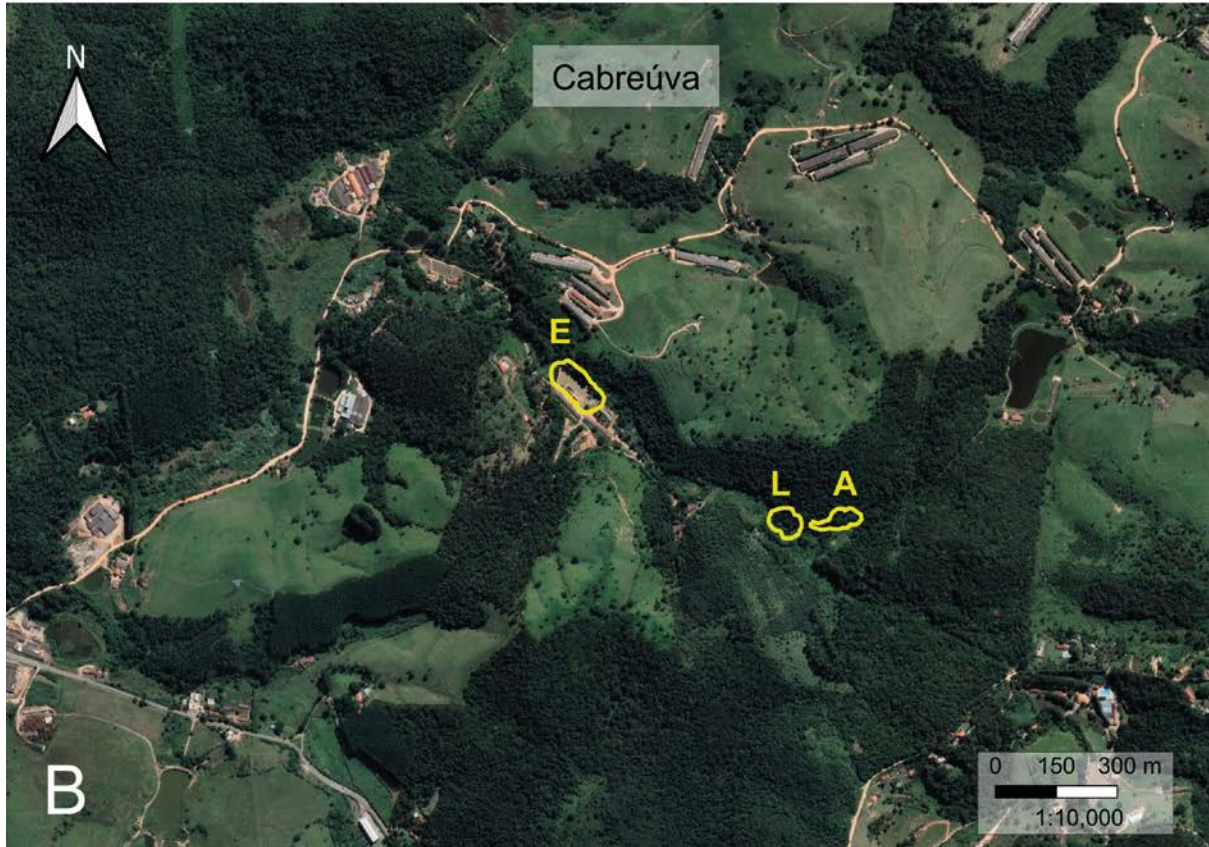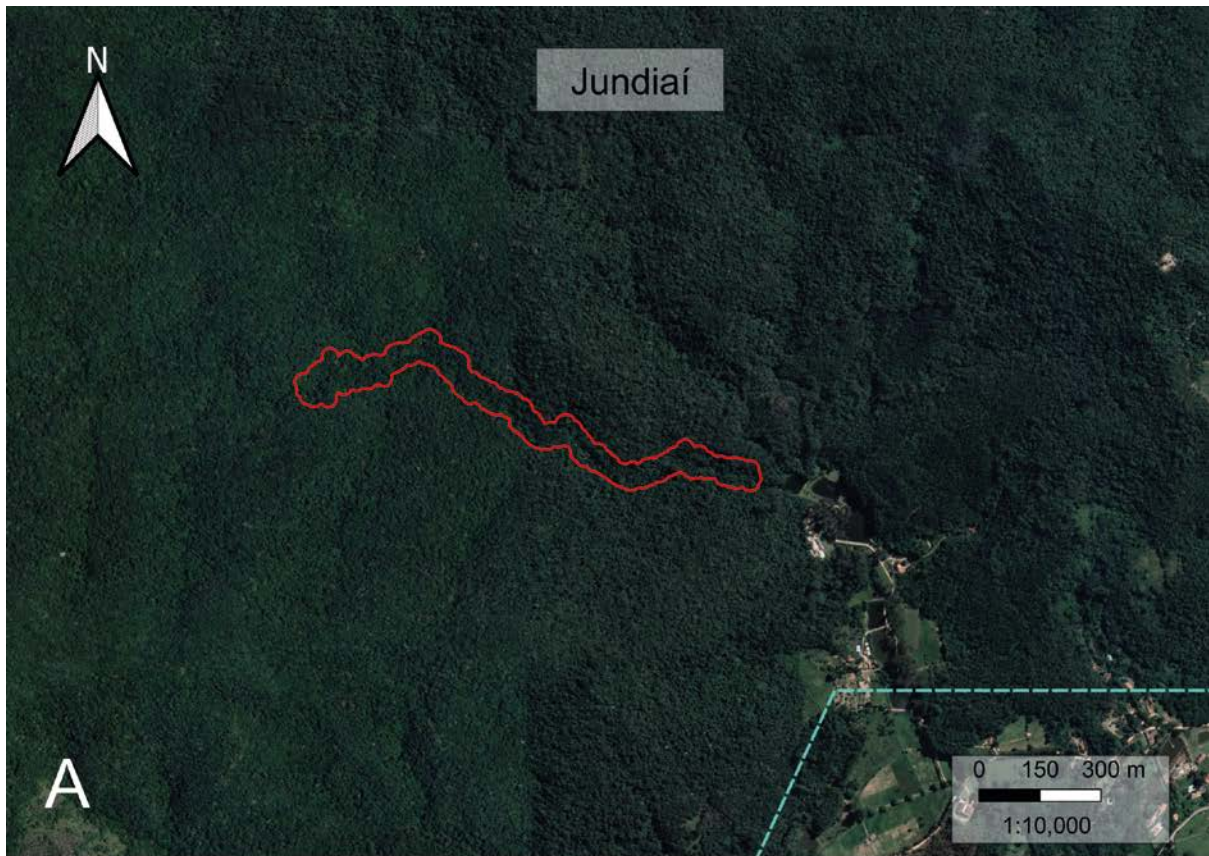
Supplementary Figure S1
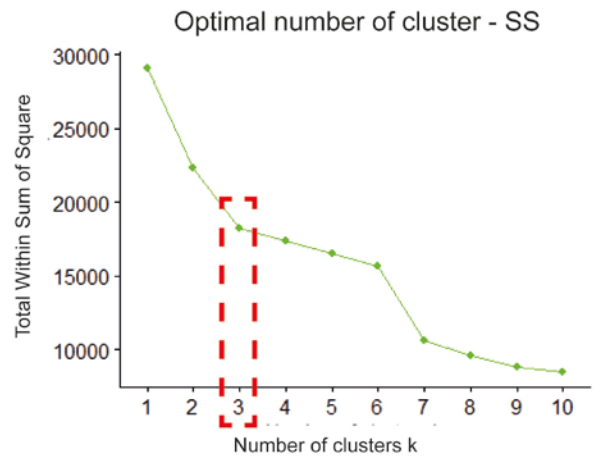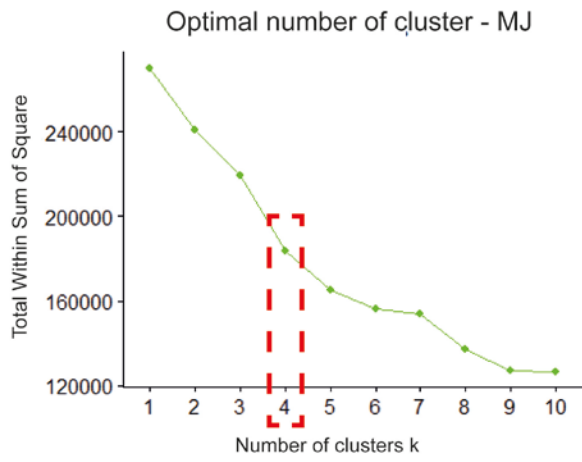
Supplementary Figure S2

Supplementary Figure S3