Optimizing speleological monitoring efforts: Insights from long-term data for tropical iron caves

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Abstract

Understanding the factors underpinning species abundance patterns in space and time is essential to implement effective cave conservation actions. Yet, the methods employed to monitor cave biodiversity still lack standardization, and no quantitative assessment has yet tried to optimize the amount and type of information required to efficiently identify disturbances in cave ecosystems. Using a comprehensive monitoring dataset for tropical iron caves, comprising abundance measurements for 33 target taxa surveyed across 95 caves along four years, here we provide first evidence-based recommendations to optimize monitoring programs seeking to follow target species abundance through time. We found that seasonality did not influence the ability to detect temporal abundance trends. However, in most species, abundance estimates assessed during the dry season resulted in a more accurate detection of temporal abundance trends, and at least three surveys were required to identify global temporal abundance trends. Finally, we identified a subset of species that could potentially serve as short-term disturbance indicators. Results suggest that iron cave monitoring programs implemented in our study region could focus sampling efforts in the dry season, where detectability of target species is higher, while assuring data collection for at least three years. More generally, our study reveals the importance of long-term cave monitoring programs for detecting possible disturbances in subterranean ecosystems, and for using the generated information to optimize future monitoring efforts.

Keywords

Iron caves, landscape ecology, mining, speleology, subterranean communities, troglobiont.

Introduction

Quantifying long-term changes in abundance of cave-dwelling organisms and identifying indicator species, reflecting the health status of subterranean ecosystems, are among the fundamental research goals of modern subterranean conservation biology (Mammola et al., 2020). For instance, the lack of knowledge about the factors underpinning abundance patterns in space and time are among the main impediments to the effective protection of cave fauna (Cardoso et al., 2011). Long-term studies in caves are scarce (Di Russo et al., 1997; Salvidio et al., 2019), and most previous efforts assessing community-level responses have evaluated population dynamics (Bichuette & Trajano, 2003; Ferreira et al., 2005; Lunghi, 2018), ecological niches (Mammola & Isaia, 2016; Mammola, Piano & Isaia, 2016), or temporal and spatial variation (Tobin, Hutchins & Schwartz, 2013; Ferreira et al., 2015; Owen et al., 2016; Paixão, Emanuelle Arantes Ferreira & Paixão, 2017; Mammola & Isaia, 2018; Ferreira & Pellegrini, 2019; Pellegrini, Faria & Ferreira, 2020). Few studies have evaluated the influence of anthropogenic disturbance on cave biodiversity (Bernardi, Souza-Silva & Ferreira, 2010; Pellegrini & Lopes Ferreira, 2012; Faille, Bourdeau & Deharveng, 2015; Cajaiba, Cabral & Santos, 2016; Pellegrini et al., 2016; Jaffé et al., 2018).

Due to the unique characteristics of subterranean environments, an important fraction of cave fauna exhibits adaptations for life in these extreme environments (Pipan & Culver, 2013). Some of these species are obligate subterranean dwellers and often comprise narrow-range endemic and threatened species (Harvey, 2002), so stringent legislation has been put in place in some countries to protect them (Harvey et al., 2011; Culver & Pipan, 2014). In Brazil, companies executing projects that could potentially impact cave ecosystems are required by law to assess the extent of impacts and implement control, monitoring and/or compensation measures (CONAMA, 1986; Decree, 2008; MMA/ICMBio, 2019). After environmental licenses are granted, some caves are included in long-term monitoring programs, ultimately seeking to detect possible disturbances on subterranean fauna. These studies generate comprehensive biological databases containing valuable information for numerous caves sampled over long periods of time (Jaffé et al., 2016, 2018; Trevelin et al., 2019). However, although many recommendations have been made to monitor cave biodiversity (Eberhard, 2001; NPS, 2015; Culver & Sket, 2016), methods still lack standardization, and no quantitative assessment has yet tried to optimize the amount and type of information required to efficiently identify disturbances in cave ecosystems. This is nevertheless essential to design systematic, repeatable, and intensive surveys of cave-dwelling organisms, allowing the formulation of evidence-based management decisions (Wynne et al., 2018, 2019).

In Brazil, most cave monitoring programs have focused on assessing temporal changes in relative abundance in a set of selected species (ativoambiental, 2019; BRANDT, 2019). However, the temporal frequency of field surveys, the impact of seasonal fluctuations in population size, and the sample sizes needed to detect temporal changes in population abundance, are yet to be systematically assessed. Moreover, the selection of species surveyed in these monitoring programs is not based on their usefulness as disturbance bio-indicators. Here we aim to fill these gaps, taking advantage of a comprehensive cave monitoring dataset containing abundance measurements for target target taxa surveyed across iron caves along four years.

Material & Methods

Study Area

The study was performed in the *Serra dos Carajás* region, southeast of the state of Pará, in the Brazilian Amazon. This region is within the limits of the *Floresta Nacional de Carajás*, a

87 protected area of 400,000 ha allowing sustainable use. The caves analyzed in this study are
88 located in two highlands known as *Serra Norte* and *Serra Sul* (Fig. 1). These two regions harbor
89 banded ironstone formations known as *cangas*, unique *campo rupestre* ecosystems resembling
90 mountain savannas (Zappi et al., 2019), and one of the world's largest deposits of iron ore
91 (Poveromo, 1999).
92
93 *Database*
94 We used data generated by independent environmental consulting companies, so our study did
95 not involve any field work. Vale S.A., a mining company, began operations in the region more
96 than two decades ago (Souza-Filho et al., 2019), and has conducted numerous caves surveys over
97 the last years as part of a large monitoring program related to environmental licensing processes.
98 All surveys where authorized by Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais
99 Renováveis (IBAMA), under licenses ABIO 455/2014 (Projeto Ferra Carajás S11D nº
100 02001.000711/2009-46) and ABIO 639/2015 (Projeto Ferro Serra Norte – Estudo Global das
101 Ampliações das minas N4 e N5 nº 02001.002197/2002-15). We compiled the data generated in
102 these surveys to collect information from 33 target taxa across 95 caves, surveyed between
103 August 2015 and September 2019. The selection of species included in these monitoring
104 programs was based on the following criteria, as stated in environmental assessment reports
105 (Vale, 2015, 2017): Large body size and easy to identify in the field, abundant and showing a
106 wide distribution range, resolved taxonomic classification (at least to the morpho-species level),
107 and short life cycles allowing the rapid detection of changes in population dynamics (see Table 1
108 for the full list of target taxa and their ecological classification). All the selected species were
109 actively surveyed during each field trip, so absences represent true absences rather than missing
110 data. In each cave, the absolute abundance of each target taxa was quantified at least once during
111 the rainy and the dry season, and sometimes multiple times in one year. Sampling was performed
112 through an active visual search throughout the caves, aiming to cover all available micro-habitats
113 (spaces under rocks, small cracks, moist soil, etc.) and organic deposits (litter, logs, carcasses,
114 guano, etc.). Animals were collected with the aid of tweezers and brushes, and all individuals
115 found in each cave were counted to estimate abundance per species, as performed in other studies
116 (Silva, Martins & Ferreira, 2011; Ferreira et al., 2015; Bento et al., 2016; Pellegrini & Ferreira,
117 2016; Paixão, Emanuelle Arantes Ferreira & Paixão, 2017; Ferreira & Pellegrini, 2019; Souza-
118 Silva, Iniesta & Ferreira, 2020).
119
120 *Environmental conditions and landscape metrics*
121 External and internal environmental conditions were monitored during the entire period across
122 caves. Monitored variables included the deviation in average bimonthly rainfall in relation to the
123 expected from a 20-years series (in mm, retrieved from small weather stations located in nearby
124 mines S11D e N4E), and mean internal temperature (ºC) on the date of the surveys (retrieved
125 from portable data loggers placed in the most distant location from cave entrances). We also
126 recorded the Area (meters^2) of each studied cave as an additional internal condition widely known
127 to influence biodiversity patterns in these ecosystems (Jaffé et al., 2016, 2018). Using 30m
128 resolution land-cover maps from 2015 to 2019 (Souza et al., 2020), we then quantified a suit of
129 landscape metrics, including the proportional amount of forest, canga and mining land covers
130 surrounding caves, and topographic distance to the nearest mine (see details in Supplemental
131 Table S1). These were all calculated at two different spatial scales (circular buffers with 500 and
132 1000 m radius), using the R packages *landscapemetrics* (Hesselbarth et al., 2019) and
133 TopoDistance (Wang, 2020). Two of these metrics directly captured possible disturbance of
134 subterranean environments that could account for changes in the abundance of the studied
135 species: Mining cover and distance to the nearest mine.

136
137   *Assessing drivers of community composition across caves*
138   Aiming to quantify how environment, cave, and landscape variables influenced overall
139   community composition, we ran a partial redundancy analysis (RDA) controlling for differences
140   between both highlands (Serra Norte and Serra Sul), using the *vegan* package (Oksanen et al.,
141   2019). The community composition matrix containing relative abundances for each taxa was used
142   as response variable and predictor variables included year, season, microclimate and landscape
143   metrics (Legendre & Legendre, 1998). The highland where caves were located was specified as a
144   conditional variable on the model to control for the effect of cave´s geographical location.
145   Microclimate and landscape variables were standardized, community composition was Hellinger-
146   transformed, and permutation tests were used to assess significance of marginal effects (Legendre
147   & Legendre, 1998).
148
149   *Assessing the influence of seasonality on the detection of temporal abundance trends*
150   One of the main goals of cave monitoring programs was to assess changes in species abundance
151   over time, and thereby identify species with declining or increasing populations in a particular
152   cave. To understand how seasonality influenced the detection of abundance trends over time, we
153   ran linear models containing the total number of observed individuals as the response variable
154   and the interaction between sampling date and season. If seasonality influences temporal
155   abundance trends, we would expect to find significant interaction terms. No significant
156   interactions, on the other hand, would indicate that the trends can be detected regardless of the
157   season when the surveys where performed. To prevent overfitting, linear models were ran for taxa
158   and caves represented by at least five surveys in each season (final sample size was 16 taxa and
159   50 caves). Given the large number of models we used the Benjamini & Hochberg approach to
160   adjust *p*-values, employing the *p.adjust* function from the stats R package (R, 2020).
161
162   *Assessing the influence of sampling effort on the detection of temporal abundance trends*
163   Given the extensive field exposure of people and elevated costs associated with cave monitoring
164   programs, it is important to quantify how the sampling effort influences the detection of temporal
165   abundance trends. To do so we compared linear model coefficients of models fitted with the full
166   dataset with those of models fitted with reduced datasets. We first split the data by season and ran
167   linear models containing the total number of observed individuals as the response variable and
168   sampling date as predictor. In these full models we included observations for all sampling dates,
169   and excluded taxa and caves represented by less than three surveys per season. We then ran linear
170   models on data subsets containing a reduced number of observations (ranging between two and
171   the maximum number of sampling dates found in each cave and taxa). For each data subset
172   containing a given number of observations (surveys) we performed ten random samplings
173   without replacement, to ensure the sampling of different sampling dates. Finally, we compared
174   coefficients from full models with those of subset models using root mean squared error (rmse),
175   implemented through the *rmse* function from the Metrics R package (Hamner & Frasco, 2018).
176   Lower values of rmse indicate more similar model coefficients.
177
178   *Identifying disturbance indicator species*
179   Given the life history variation between species and their different susceptibility to habitat
180   disturbance, it is essential to identify indicator species that show a rapid response to disturbance
181   in order to optimize monitoring programs. By focusing on these indicator species, monitoring
182   programs could survey caves more efficiently, thereby making resources available to study more
183   caves or other aspects of cave biodiversity requiring attention. Here we tried to identify
184   disturbance indicator species by assessing the relationship between disturbance metrics and

185 species abundance patterns. We first modeled patterns of relative abundance across all caves,
186 using the function *manyglm* from the R package mvabund (Wang et al., 2012). It uses a
187 multivariate generalized linear model (GLM) to make inferences by fitting separate GLMs to a
188 common set of explanatory variables, and testing significance through resampling-based
189 hypothesis testing. We ran negative binomial GLMs containing abundance as the response
190 variable and sampling season nested in year, distance to mine and mining cover as predictor
191 variables. Significance *p*-values were calculated using 999 resampling iterations via PIT trap
192 resampling, adjusted for multiple testing using a step-down resampling procedure (Wang et al.,
193 2012). We then used univariate coefficient estimates and significance for individual species, to
194 identify specific responses to disturbance metrics (distance to mine and mining cover).
195   We then assessed the relationship between disturbance metrics and temporal trends in
196 species abundance within each cave. To do so we ran linear models containing the total number
197 of observed individuals as the response variable and sampling date as predictor, excluding taxa
198 and caves represented by surveys spanning less than three years (some caves where surveyed
199 multiple times in a single year but these where only included in this analysis if surveys spanned at
200 least three different years). We then used the model coefficients for each species at each cave,
201 representing temporal abundance trends (positive coefficients showing an increase and negative
202 coefficients a decrease in abundance through time), to run a second set of linear models
203 regressing temporal abundance trends on disturbance metrics. These second set of models thus
204 contained as response variable the model coefficients representing temporal abundance trends for
205 each species at each cave, and distance to mine and mining cover (at different spatial and
206 temporal scales) as predictors. To prevent overfitting we excluded species represented by less
207 than ten coefficients (caves), and only constructed models containing a single predictor. We then
208 ran likelihood-ratio tests, where we compared each model with a null model containing no
209 predictors, and selected those predictor variables resulting in a significant decrease in the model's
210 log-likelihood. Finally, we retrieved and plotted coefficients and *p*-values for these best-fitting
211 models. All data and R scripts are available in GitHub
212 (https://github.com/rojaff/cave_monitoring).
213
214 **Results**
215
216 Overall community composition was weakly influenced by seasonality, cave size, environmental
217 conditions, and the composition and configuration of landscapes surrounding caves, as more than
218 87% of variance in community composition remained unexplained by these factors (Table 2).
219   Seasonality did not influence the ability to detect species abundance trends over time, since
220 the interaction effect between sampling date and season was not significant in any taxa nor cave
221 (Fig. 2). Increasing the number of samples resulted in more similar model coefficients between
222 full and subset models, and root mean squared errors usually stabilized after three surveys (Fig.
223 3). However, in most species the dry season datasets allowed a more accurate detection of
224 temporal abundance trends, as revealed by lower root mean squared errors (Fig. 3).
225   Whereas relative abundance was associated to at least one disturbance metric in 22 species
226 (Fig. 4), temporal trends in abundance were found associated with disturbance metrics in only
227 five species (Fig. 5). Overall, two taxa displayed consistent responses across effects, which
228 makes them potential indicator species for cave monitoring programs: The troglobiont *Charinus*
229 *ferreus*, which appeared negatively affected by disturbance, and a species belonging the
230 Theraphosidae family, which seem to be favored by disturbance (Table 3).
231

Discussion

234 By analyzing abundance measurements for 33 target taxa surveyed across 95 caves along four
235 years, we found that overall community composition was weakly influenced by seasonality, cave
236 size, environmental conditions, and the composition and configuration of landscapes surrounding
237 caves. Furthermore, our results show that seasonality did not influence the ability to detect
238 abundance trends over time. However, in most species, abundance estimates assessed during the
239 dry season resulted in a more accurate detection of temporal abundance trends, and at least three
240 surveys were required to identify global temporal abundance trends. Finally, we identified a
241 subset of species that could potentially serve as short-term disturbance indicators, some showing
242 consistent responses in different analyses.
243   Subterranean communities have been shown to be affected by seasonality, environmental
244 conditions, cave characteristics, and the structure of surrounding landscapes (Simões, Souza-
245 Silva & Ferreira, 2015; Pellegrini et al., 2016; Bento et al., 2016; Mammola & Isaia, 2018;
246 Salvidio et al., 2019; Pellegrini, Faria & Ferreira, 2020; Rabelo, Souza-Silva & Ferreira, 2020).
247 However, our results reveal that overall community composition was only weakly influenced by
248 these factors, as our model explained merely 13% of total variation in community composition
249 (Table 2). In contrast, previous work have found that cave morphology, microclimate, cave depth,
250 and sampling date explain up to 50% of the variation in community structure in limestone and
251 marble caves (Tobin, Hutchins & Schwartz, 2013; Lunghi, Manenti & Ficetola, 2014). Our
252 results thus suggest that other factors, not considered in our analyses, play an important role
253 structuring subterranean communities of iron caves. Inter-specific interactions, for instance, are
254 known to have a profound influences on community structure (Ferreira & Martins, 1999;
255 Mammola, Piano & Isaia, 2016). Alternatively, biological samples collected in iron caves may
256 not capture the dynamics of the entire subterranean habitat, comprised by a network of fissures
257 and voids and traditionally referred to as *Milieu Souterrain Superficiel* (MSS) (Culver & Pipan,
258 2014; Mammola et al., 2016; Mammola, 2018). For instance, most of the surveyed caves were
259 larger than 5x5 m (Fig. S1), so they did not represent suitable sampling sites for the MSS
260 (Mammola et al., 2016).
261   Even though seasonality affected overall community composition, it did not influence the
262 ability to detect species abundance trends over time. External climatic conditions are increasingly
263 attenuated at higher cave depths (Tobin, Hutchins & Schwartz, 2013), so species occurring in the
264 inner portions of caves appear to have life cycles decoupled from external seasons, whereas
265 species inhabiting the outermost portions of caves seem to be more strongly affected by
266 seasonality (Di Russo et al., 1997; Gunn, Hardwick & Wood, 2000; Bichuette & Trajano, 2003;
267 Ferreira et al., 2015; Mammola, Piano & Isaia, 2016; Lunghi, 2018). Recognizing the impact of
268 seasonality on species detection, the current Brazilian legislation stipulates that cave biodiversity
269 surveys need to comprise at least two sampling events, one during the dry and one during the
270 rainy season (MMA, 2017). It is worth emphasizing that these sampling requirements targeted a
271 more accurate estimation of species richness, but not the continuous monitoring of focus species
272 in time. Two sampling events are likely insufficient to obtain reliable species richness estimates
273 for highly diverse caves (Auler & Piló, 2015; Wynne et al., 2018), so some authors have argued
274 for the estimation of optimal sample sizes based on species accumulation curves (Trajano &
275 Bichuette, 2010; Trajano, 2013). Our results provide the first evidence-based recommendations to
276 optimize sampling efforts of monitoring programs seeking to assess target species abundance
277 through time. Specifically, our findings suggest that monitoring efforts aiming to detect changes
278 in abundance through time do not need to sample during two different seasons each year (Fig. 2).
279 Sampling efforts of such monitoring programs could thus be optimized by performing more
280 focused surveys and by surveying a larger number of caves during the same period each year.

281   Importantly, restricting sampling to a single season could substantially attenuate the negative
282   impact of cave visitation by researchers on subterranean communities (Pellegrini & Ferreira
283   2016, Pellegrini & Lopes Ferreira 2012, Bernardi et al. 2010).
284   Although the composition and spatial distribution of subterranean communities can
285   remain constant over periods of several years (Salvidio et al., 2019), our results suggest that
286   sampling during at least three years is necessary to detect temporal changes in abundance patterns
287   in most of our focus species (Fig. 3). We note that our dataset only spans a period of four years
288   (although some caves were sampled multiple times during the same season/year), so it cannot
289   capture longer temporal changes in abundance. We also caution that these results cannot be
290   generalized to all subterranean fauna, as different life histories and generation times will
291   ultimately determine how fast these organisms respond to disturbances (Ferreira, 2005;
292   Mammola et al., 2016; Culver & Pipan, 2019). Sampling in different seasons did not influence
293   the ability to detect general abundance trends over time, but the dry season datasets allowed a
294   more accurate detection of temporal abundance trends in most species. These results suggest
295   higher detection probabilities in the dry season for the subset of species where RMSE curves
296   show a steeper decrease during the dry season (Fig. 3). Interestingly, this was the case for the
297   troglobitic amblypygid *Charinus ferreus*, a species that is difficult to detect like other
298   troglobionts (Wynne et al., 2018; Lunghi, 2018). Our results thus suggest that monitoring
299   programs focusing on terrestrial subterranean fauna from our study region could concentrate
300   sampling activity in the dry season, where most species seem to be easier to detect. Likewise, our
301   findings highlight the importance of implementing long-term monitoring efforts spanning at least
302   three years.
303   The concept of indicator species in ecosystem management relies on the idea of
304   identifying taxa responsive to environmental change, that could inform policies, protocols, and
305   best practices (Carignan & Villard, 2002). Such environmental indicators (McGeoch, 1998) seek
306   to provide cost and time effective guidelines to address pressing conservation issues, such as
307   those faced by large-scale mining projects (Sonter, Ali & Watson, 2018). Assessing the response
308   of subterranean fauna to anthropogenic disturbance nevertheless requires access to long-term
309   cave monitoring datasets, which are remarkably rare for tropical caves (McGeoch, 1998;
310   Carignan & Villard, 2002; Mammola et al., 2020). Here we identified 20 taxa where overall
311   abundance responded to cave disturbance, and five where temporal abundance trends where
312   associated with disturbance. Only two taxa displayed consistent responses across effects, which
313   makes them candidate indicator species for cave monitoring programs: *Charinus ferreus* and a
314   species belonging the Theraphosidae family (Table2). Both are arachnids, a group that was
315   recently identified as biodiversity indicator for iron caves (Trevelin et al., 2019). Being a top
316   predator restricted to cave ecosystems, the first species is a well-known troglobitic Amblypygi
317   (Giupponi & de Miranda, 2016). Its strong and consistent response to disturbances (Figs. 4 and 5)
318   suggest the species is associated with pristine and undisturbed ecosystems, which makes it an
319   ideal disturbance indicator. Theraphosidae spiders, on the other hand, are sedentary sit-and-wait
320   predators from the epigea, rarely occupying subterranean environments for reproduction or
321   shelter (Fonseca-Ferreira, Zampaulo & Guadanucci, 2017). Our results suggest that they
322   apparently benefit from disturbance to opportunistically colonize caves, or alternatively, that
323   disturbances in the surrounding external habitats are forcing them to look for shelter inside the
324   caves. The species nevertheless awaits formal taxonomic description, which currently limits its
325   usefulness as an indicator species.
326   Effect sizes of disturbance on overall abundance and temporal abundance trends where
327   generally small, suggesting that some effects could have remained undetected because they
328   would require sampling over longer time periods (Di Stefano, 2001; Legg & Nagy, 2006). For
329   instance, the ability to detect trends in tropical bat population abundance was shown to be

330 dependent on the duration of the monitoring efforts, and only long programs (> 20 years) showed
331 sufficient statistical power to reliably detect abundance trends (Meyer et al., 2010). This could
332 explain why some of our focus species did not exhibit coherent responses across analyses, like
333 the troglobionts *Pyrgodesmidae* sp. and *Escadabiidae* sp., or opportunistic colonizers like the
334 anuran *Leptodactylus pentadactylus* or *Pristimantis fenestratus*. Although empirical evidence
335 from long-term cave monitoring efforts focusing on invertebrates is scarce (Faille, Bourdeau &
336 Deharveng, 2015; Cajaiba, Cabral & Santos, 2016; Owen et al., 2016), our results thus suggest
337 that longer monitoring efforts are needed to detect disturbance responses in most cave-dwelling
338 species.
339
340 Conclusions
341
342 Our study reveals the importance of long-term cave monitoring programs for detecting possible
343 disturbances in subterranean ecosystems, and for using the generated information to optimize
344 future monitoring efforts. Results show that iron cave monitoring programs implemented in our
345 study region could focus sampling efforts in the dry season, where detectability of target species
346 is higher, while assuring data collection for at least three years. *Charinus ferreus* was identified as
347 the most promising short-term disturbance indicator species.
348

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350
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566

List of surveyed taxa and their ecological classification.

1   **Table 1:** List of surveyed taxa and their ecological classification.

Class	Order	Family	Species	Ecological Classification
Malacostraca	Isopoda	Scleropactidae	*Circoniscus carajasensis Campos-Filho & Araujo, 2011*	Troglobiont
Amphibia	Anura	Craugastoridae	*Pristimantis cf. fenestratus (Steindachner, 1864)*	Trogloxene
		Leptodactylidae	*Leptodactylus pentadactylus (Laurenti, 1768)*	Accidental
Arachnida	Amblypygi	Phrynidae	*Heterophrynus longicornis Butler, 1873*	Troglophile
		Charinidae	*Charinus ferreus Giupponi & Miranda, 2016*	Troglobiont
	Araneae	Araneidae	*Alpaida sp.1*	Troglophile
		Pholcidae	*Mesabolivar spp.*	Troglophile
		Prodidomidae	Prodidomidae sp.	Troglobiont
		Salticidade	*Astieae sp.1*	Troglophile
		Scytodidae	*Scytodes eleonorae Rheims & Brescovit, 2001*	Troglophile
		Theraphosidae	Theraphosidae	Troglophile
		Theridiosomatidade	*Plato spp.*	Troglophile
	Opiliones	Cosmetidae	*Roquettea singularis Mello-Leitão, 1931*	Troglophile
			Roquettea sp.	Troglophile
		Escadabiidae	Escadabiidae sp.1	Troglobiont
			Escadabiidae sp.2	Troglobiont
		Gagrellinae	*Prionostemma sp.*	Troglophile

		Stygnidae	*Protimesius sp.*	Troglophile
			Stygnidae sp.1	Troglophile
Chilopoda	Scutigeromorpha	Pselliodidae	*Sphendononema guildingii (Newport, 1845)*	Troglophile
Diplopoda	Glomeridesmida	Glomeridesmidae	*Glomeridesmus cf. spelaeus Iniesta, Ferreira & Wesener, 2012*	Troglobiont
	Polydesmida	Chelodesmidae	Chelodesmidae sp.	Troglophile
		Pyrgodesmidae	Pyrgodesmidae sp.1	Troglobiont
	Spirostreptida	-	Spirostreptida sp.	Troglophile
		Pseudonannolenidae	*Pseudonannolene cf. spelaea Iniesta & Ferreira, 2013*	Troglobiont
Insecta	Coleoptera	Dytiscidae	Dytiscidae sp.1	Stygobiont
	Hemiptera	Cydnidae	Cydninae sp.1	Troglophile
		Reduviidae	Emesinae sp.	Troglophile
	Lepidoptera	Erebidae	*Latebraria sp.*	Trogloxene
	Orthoptera	Phalangopsidae	*Phalangopsis ferratilis Junta, Castro-Souza & Ferreira, 2020*	Troglophile
			Uvaroviella sp.	Troglophile
Mammalia	Rodentia	Cricetidae	*Rhipidomys sp.*	Undefined
Reptilia	Squamata	Phyllodactylidae	*Thecadactylus rapicauda (Houttuyn, 1782)*	Undefined

4 2

Summary of partial Redundancy Analyses (RDA).

The table shows F-statistics and p-values from permutation tests (adjusted $r^2 = 0.13$).

1 **Table 2:** Summary of partial Redundancy Analyses (RDA). The table shows F-statistics and *p*-
2 values from permutation tests (adjusted $r^2 = 0.13$).

Variable	Df	Variance	F	*Pr(>F)*
Season nested in year	1	0.0018	4.408	0.001***
Canga cover	1	0.0005	1.164	0.285
Forest cover	1	0.0008	2.093	0.055*
Mining cover	1	0.0010	2.378	0.034*
Distance to mine	1	0.0027	6.766	0.001***
Area	1	0.0197	48.696	0.001***
Temperature	1	0.0054	13.408	0.001***
Dev Rainfall	1	0.0002	0.604	0.746
Residual	671	0.2710		

1   1

Taxa displaying significant responses to disturbance metrics, considering overall abundance and temporal abundance trends.

Taxa showing consistent responses (highlighted in bold) are suggested as short-term

disturbance indicators. The best sampling season (according to Fig. 3), is indicated for each

taxa.

1 **Table 3:** Taxa displaying significant responses to disturbance metrics, considering overall
2 abundance and temporal abundance trends. Taxa showing consistent responses (highlighted in
3 bold) are suggested as short-term disturbance indicators. The best sampling season (according to
4 Fig. 3), is indicated for each taxa.

Taxon	Abundance		Temporal abundance trend		Sampling
	Distance to mine	Mining cover	Distance to mine	Mining cover	
Charinus ferreus*	-	**Negative**	**Positive**	**Negative**	**Dry**
Theraphosidae	**Negative**	**Positive**	-	**Positive**	**Dry**
Uvaroviella sp.	Negative	-	Positive	Negative	Both
Rhipidomys sp.	-	-	Positive	-	Dry
Roquettea sp.	-	-	-	Positive	Rain
Pyrgodesmidae sp.1*	-	Negative	-	-	Rain
Spirostreptida sp.1	Positive	-	-	-	Rain
Prodidomidae sp.*	Positive	Negative			Dry
Escadabiidae sp.1*	Negative	Negative	-	-	Rain
Escadabiidae sp.2*	Positive	-	-	-	Rain
Leptodactylus pentadactylus	Negative	-	-	-	Both
Pristimantis fenestratus	Negative	Positive	-	-	Dry
Thecadactylus rapicauda	-	Negative	-	-	Dry
Plato spp.	Negative	-	-	-	Dry
Sphendononema guildingii	-	Positive	-	-	Dry
Astieae sp.1	Negative	-	-	-	Dry
Protimesius sp.	Negative	-	-	-	Rain
Prionostemma sp.	Negative	Positive	-	-	Dry
Stygnidae sp1	-	Positive	-	-	Dry
Phalangopsis sp.1	-	Positive	-	-	Dry

6 * Troglobitic species

Figure 1

Location of the study region (upper left corner) and a detail of the study area showing the spatial distribution of the caves included in our analyses (N = 95), colored by the number of surveys performed in each.

While the hillshade layer was constructed using a digital elevation model (SRTM, 1 arc-second) from USGS Earth Explorer, the land use classification shapefile was obtained from Souza-Filho et al. (2019). Coordinates are shown in decimal degrees.
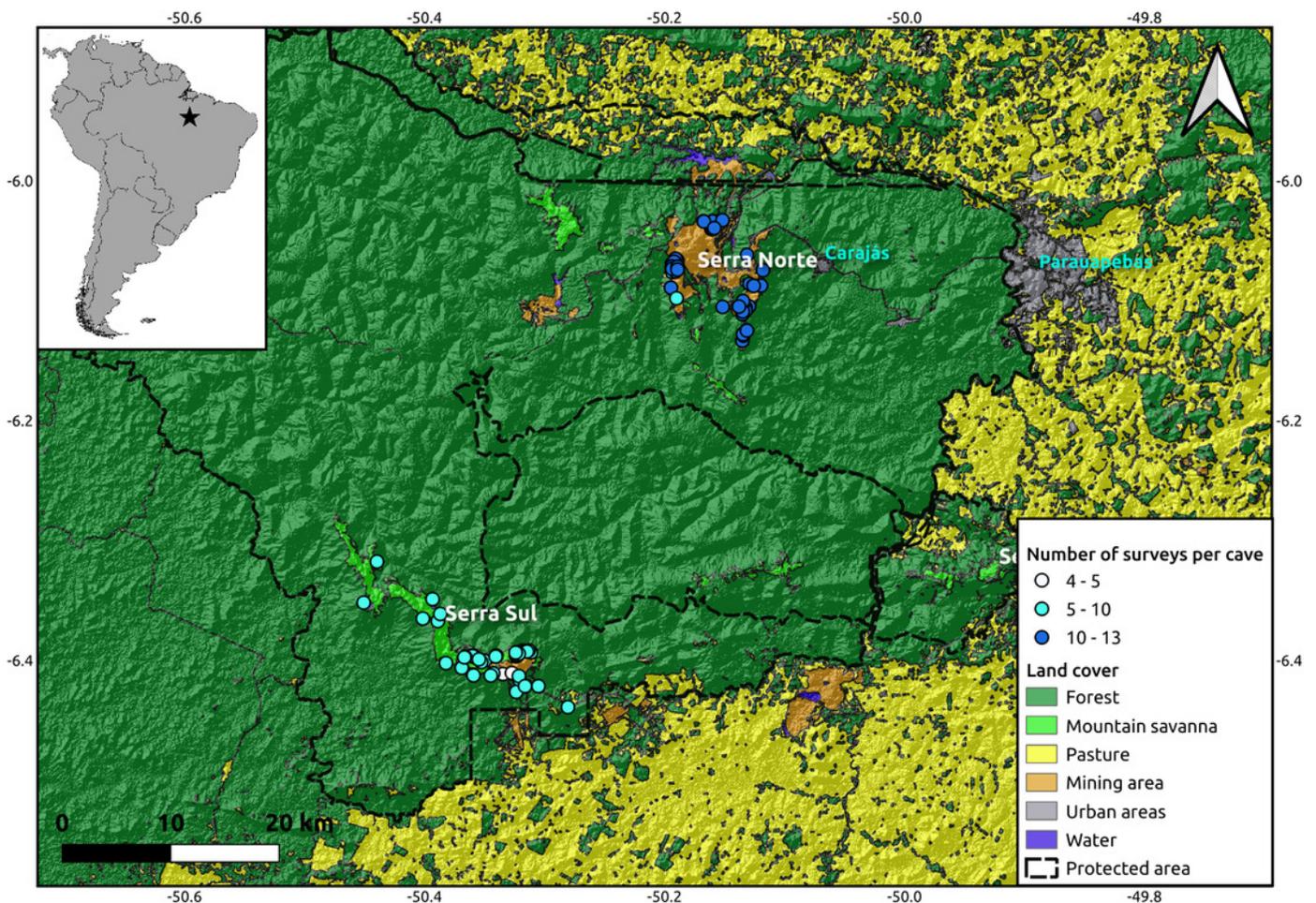
Figure 2

Adjusted *p*-values for the interaction between sampling date and season across 16 taxa and 50 caves.

The Benjamini & Hochberg approach was used to adjust *p*-values and the red horizontal line shows the threshold value of 0.05 (values above this line represent cases where the interaction effect was not significant).
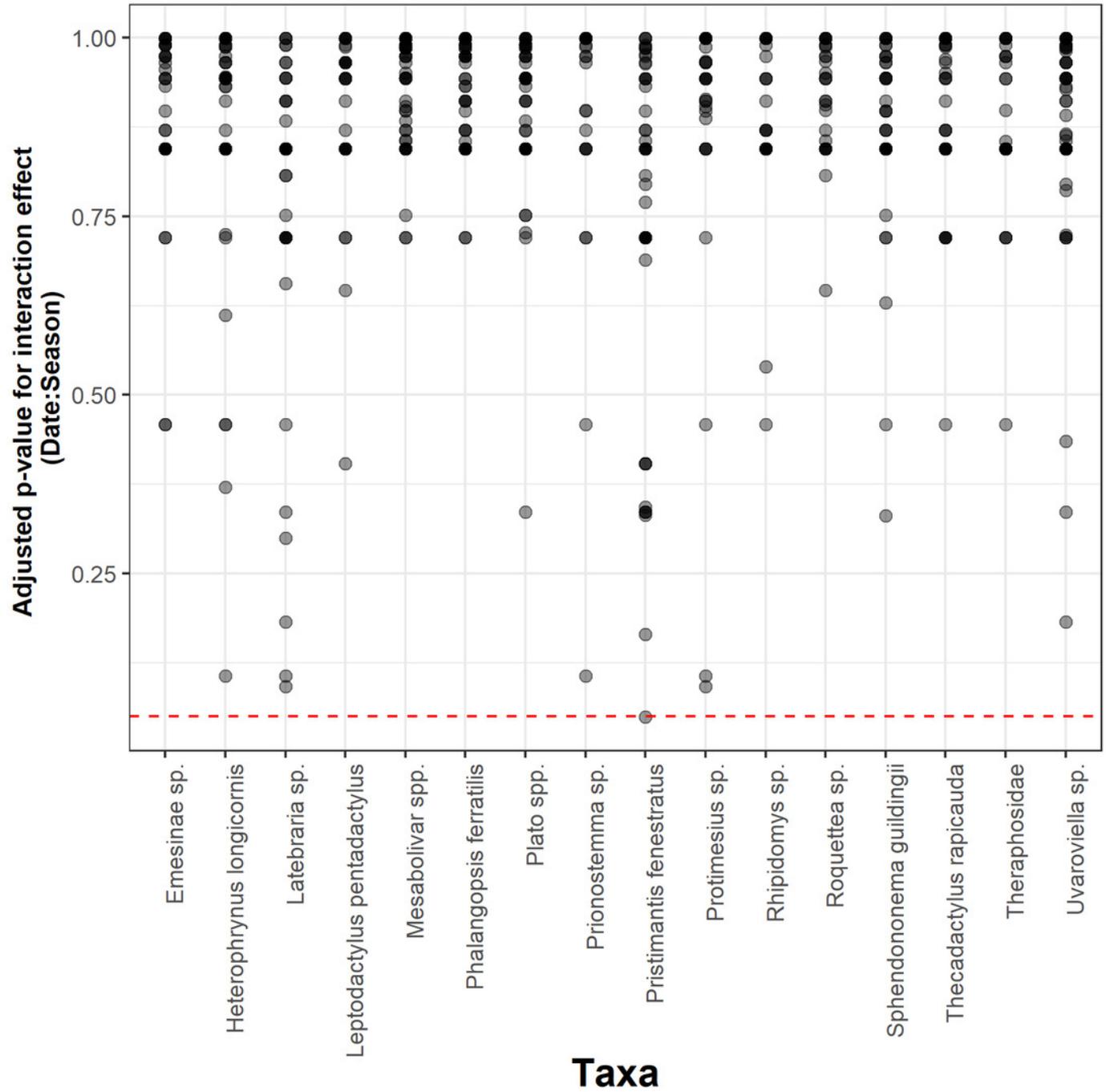
Figure 3

Root mean squared error (rmse) for model coefficients from full models and those of subset models containing reduced numbers of samples.

Lower values of rmse indicate more similar model coefficients (and a more reliable estimation of temporal abundance trends). For each data subset containing a given number of observations (surveys) we performed ten random samplings without replacement, to ensure the sampling of different sampling dates.
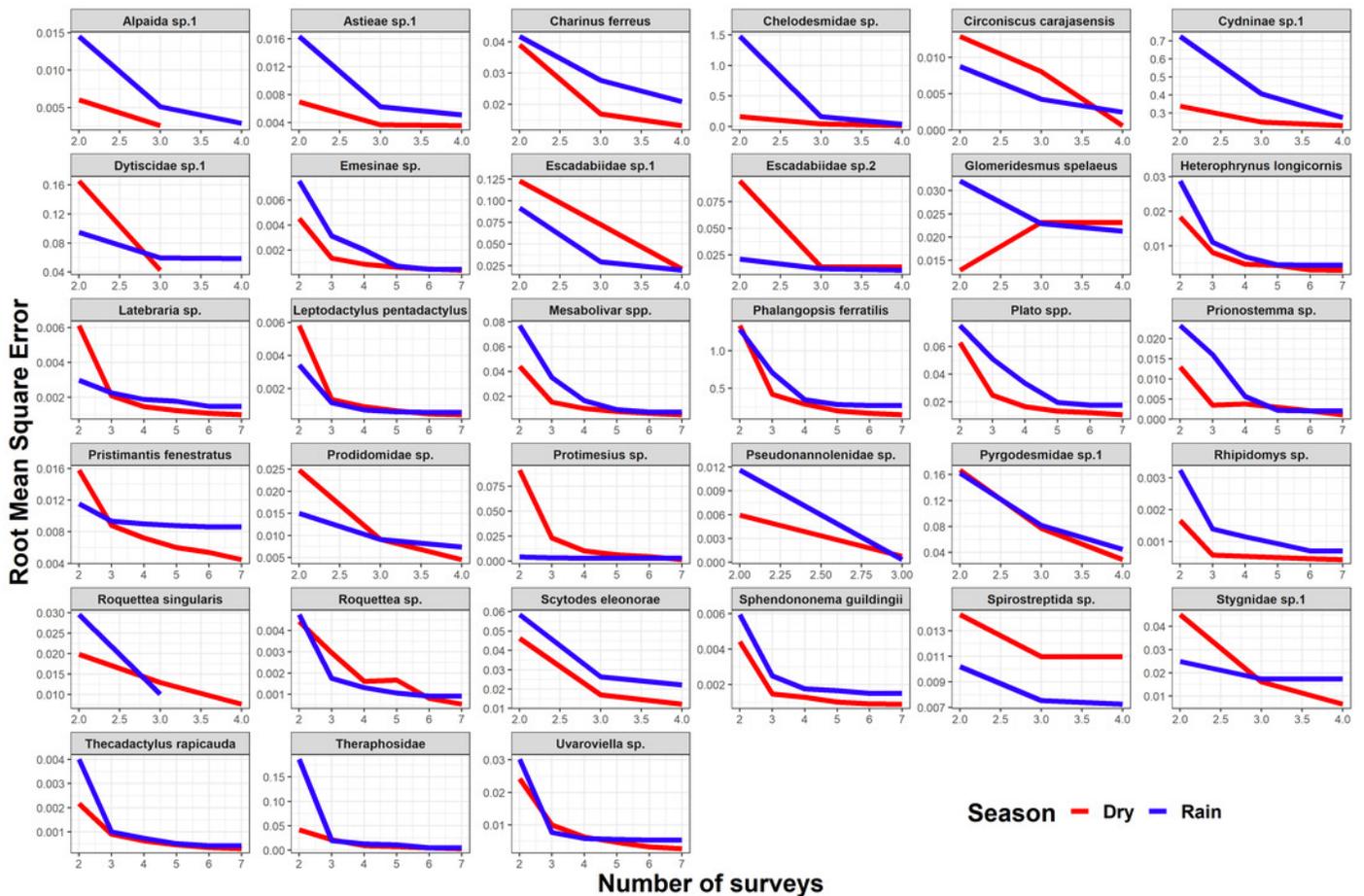
Figure 4

Model coefficients and 95% confidence intervals for species showing significant associations between overall abundance and two disturbance metrics.
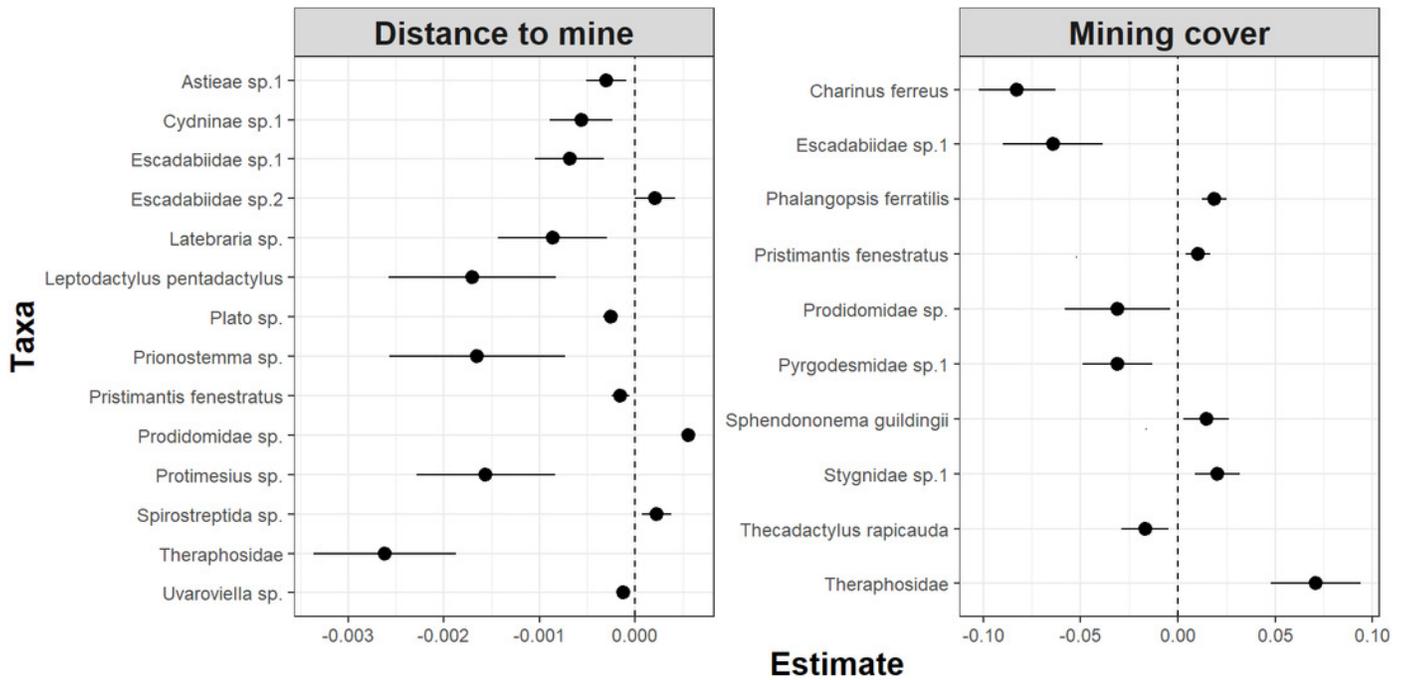
Figure 5

Model coefficients and 95% confidence intervals for species showing significant associations between temporal abundance trends and two disturbance metrics.