ABEL PERIGOLO MÓL

HOW MANY SPECIES? ECOLOGICAL DRIVERS OF CRICKET (ORTHOPTERA: GRYLLOIDEA) DIVERSITY

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

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APROVADA: 24 de fevereiro de 2012.

Prof. Edson Zefa

Prof^{a}. Flávia Maria da Silva Carmo

Prof. Carlos Frankl Sperber
(Orientador)

"I love fools' experiments. I am always making them."

Charles Darwin

Aos meus pais,

pelo amor, apoio e confiança incondicionais.

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RESUMO

MÓL, Abel Perigolo, M. Sc., Universidade Federal de Viçosa, fevereiro de 2012. **Quantas espécies? Determinantes ecológicos da diversidade de grilos (Orthoptera: Grylloidea).** Orientador: Carlos Frankl Sperber.

No capítulo 1, este estudo investiga os determinantes da diversidade e abundância de grilos de serapilheira, e as possíveis interações com feições geomorfológicas. Ainda, nós propomos uma abordagem analítica que inclui amostragem local passiva como uma explicação necessária para a variação da diversidade e evidencia eventuais efeitos do ambiente nas relações diversidade-abundância. Concluímos que os processos biológicas regulando o número de espécies de grilos não são diretamente afetados por feição geomorfológica. A riqueza local é mais provavelmente limitada por processos amostrais do pool regional. No capítulo 2, avaliamos se a diversidade de gêneros de grilos sul-americanos pode ser empiricamente explicada por área de distribuição e tamanho corporal. Analisamos as espécies reportadas pela Orthoptera Species File para a região Neotropical e estimamos a área de distribuição e biomas interceptados para cada gênero. A diversidade aumenta com a área, mas o aumento é maior em áreas descontínuas. A diversidade aumenta com tamanho corporal e área tanto em áreas contínuas quanto em áreas descontínuas. A distribuição descontínua podem ou subestimar a distribuição verdadeira ou superestimar o escopo do gênero. O aumento da diversidade com tamanho corporal foi contrário às nossas expectativas. Isso pode ser resultado de efeito amostral, isto é, grilos maiores são mais facilmente amostrados e identificados. Concluímos que a distribuição de dados de grilos, embora incipiente, são relevantes para explicar diversidade de espécies entre gêneros. Os processos biológicos envolvidos nas relações empíricas merecem melhor investigação.

ABSTRACT

MÓL, Abel Perigolo, M. Sc., Universidade Federal de Viçosa, February 2012. **How many species? Ecological drivers of cricket (Orthoptera: Grylloidea) diversity.** Advisor: Carlos Frankl Sperber.

On chapter 1, this study investigates drivers of the diversity and abundance of litter crickets, and their possible interactions with the geomorphological feature. Moreover, we propose an analytical approach which includes local passive sampling as a necessary explanation for diversity variation and thus highlights eventual effective influence of environment on diversity and diversity-abundance relationship. It is concluded that the biological processes regulating number of species are not directly affected by the geomorphological feature. Local richness is most probable limited solely by a sampling process of the regional pool, and sample size is determined by factors affecting all species equally, in other words, affect the number of individuals. At Chapter 2, we aimed to evaluate if genus diversity of South-American crickets (Orthoptera: Grylloidea) may be empirically explained by distribution area and body size. We analyzed all species reported in the Orthoptera Species File with geographic distribution range reported for the Neotropics. We estimated reported distribution area, as well as intercepted biome area for each genus. Diversity increased with area, but this increase was higher and steeper in discontinuous than continuous areas. Diversity increased with body and area in both continuous and discontinuous distribution areas. Discontinuous distribution records may either underestimate actual distribution area, or overestimate the genus scope. The increase of diversity with body size was opposite to our expectations. This could result from sampling effect, where larger cricket species with smaller body size would be under-represented due to taxonomic issues. We conclude that cricket distribution data, although sparse and not-systematic, are relevant to explain species diversity among genera. The biological processes involved in the empirical relationships deserve further investigation.

GENERAL INTRODUCTION

Ecological theory predicts several mechanisms that might drive diversity. Local diversity is the result of processes occurring at different spatial scales: ecological interactions, such as competition and predation, are predominant at local level, while historical and evolutionary processes prevail at regional scale (Schluter & Ricklefs, 1993). One way to assess processes on a regional scale is comparing geographic regions with different evolutionary histories (Cadle & Greene, 1993), which requires large-scale geographic sampling. An alternative way is to compare adjacent habitats with different evolutionary histories (Soares, 2002), for instance, comparing distinct geomorphological features, which have undergone different processes of soil genesis, and has different times of existence (Ross, 2000).

Despite the bewildering variety of potential diversity drivers, some attempts to synthesize them into unifying schemes may prove fruitful. One of them is Hubbell's (2001) neutral theory of biodiversity. It explains species diversity resulting from a provisionary equilibrium among demographic stochasticity, speciation and dispersion. On local scale, Scheiner and Willig (2005) proposed a unified theory to explain diversity gradients, from which the first two propositions are particularly relevant for this study: (i) variation in environmental factors affects the number of individuals, and (ii) given a uniform environment, with fixed area, more individuals leads to more species. The latter corresponds to the passive sampling or random placement (Coleman, 1981) process that explains diversity increase with increase in number of individuals in an homogeneous area. With random placement of the individuals, we consider it the most parsimonious explanation for diversity variation. Although several studies have discussed the relationship of diversity with number of individuals, their main focus is on the comparison of datasets with different sampling effort (Gotelli & Collwell, 2001), or the estimation of total number of species in the sampled universe (Beck & Schwanghart, 2010).

Whichever process drives diversity, it is commonly measured by number of species (we restrict “diversity” hereafter to species counts). There are 1268 species of crickets described for South America, of which 195 for Brazil (Eades *et. al.*, 2012). Crickets are diverse in the neotropics (Alexander, 1968; Desutter-Grandcolas, 1992), and wide distributed, occupying all biomes, from ground level to canopy of trees (Desutter-Grandcolas, 1992).

Knowing how many species are there is a challenging question by itself. Knowing how the predictions have been made may give us clues to figure out what are the real drivers of diversity. Moreover, it can be useful to realize what may be fundamental in speciation or extinction processes. Using a why question, such as “Why are there more species in some taxa than in others?”, give us the possibility of discussing mechanisms that lead to diversity.

In a bewildering diversity of organisms, some genera are way more diverse than others. Grylloidea is not an exception. For example, while *Acantoluzarida* is a monospecific genus (*Acantoluzarida nigra* Desutter-Grandcolas), *Gryllus* has 93 described species.

Crickets are hemimetabolous and oviparous insects and an important component of forest litter macrofauna (Sperber *et al*., 2003). The oviposition can be done both in the ground and in plant tissues. The juvenile instars generally share the same habitat and resources with adults (Alexander, 1968). Most crickets hide during the day under fallen logs, rocks, leaf litter or in holes in the ground. They are traditionally regarded as omnivorous due to the acceptance of diverse food items in captivity (Walker & Masaki, 1989). In the field, many crickets are predominantly herbivores (Evans *et al.*, 1965), feeding on leaves and supplementing their diet with animal tissue. On this context, litter can provide food resources for crickets, like newly fallen leaves, flowers, fungi, fruits (Gangwere, 1961), and may represent shelter from predation. The space in the litter may form different microhabitats for crickets, reducing interspecific competition.

At this study we focused on testing if genus diversity of crickets may be empirically explained by distribution area and mean body size, which would be an indirect measure of overall abundance. We also intended to evaluate environmental drivers of abundance and species richness of forest litter crickets.

GENERAL CONCLUSIONS

The biological processes regulating number of species are not directly affected by the geomorphological feature. Local richness is most probable locally limited solely by a sampling process of the regional pool, and sample size is determined by factors affecting all species equally, in other words, affect the number of individuals.

The analytical approach we propose here highlights potential mechanisms capable of explaining empirically observed responses of species diversity to environmental drivers, and generates novel insights that cannot be obtained from previous empirical studies.

We conclude that the avaiable cricket distribution data, although sparse and not-systematic, are relevant to explain species diversity among genera. The biological processes involved in the empirical relationships that we highlighted deserve further investigation.

UNIVERSIDADE FEDERAL DE VIÇOSA
POSTGRADUATE PROGRAMME IN ENTOMOLOGY

CHAPTER ONE

Regulation of litter crickets (Orthoptera: Grylloidea) diversity: testing the interaction of ecological with geomorphological drivers

Master Dissertation

Abel Perigolo Mól

Carlos Frankl Sperber
Advisor

VIÇOSA
2012

ABSTRACT

This study investigates drivers of the diversity and abundance of litter crickets, and their possible interactions with the geomorphological feature. Moreover, we propose an analytical approach which includes local passive sampling as a necessary explanation for diversity variation and thus highlights eventual effective influence of environment on diversity and diversity-abundance relationship. We suggest some explanatory hypotheses: 1: The abundance of crickets increases with food resource availability; 2: The abundance of crickets increases with shelter availability, represented by litter depth.; 3 or Biological Neutral Hypothesis: Crickets species richness increases with number of individuals; 4: Cricket species richness is affected both by passive sampling and geomorphological feature, leading to an interaction of number of individuals and geomorphological feature on cricket species richness. A total of 2046 crickets belonging to 23 species and 6 families were collected. We did not detect any difference of cricket diversity itself among geomorphologies ($F_{1, 28} = 3.892$, $P = 0.058$,). On the other hand, we detected a significant interaction of geomorphologic feature with cricket abundance, as a co-variable, affecting cricket species richness ($F_{1,26}=7.01$; $P=0.01$). It is concluded that the abundance of crickets increases with shelter availability, which varies on different geomorphological features. Also, the biological processes regulating number of species are not directly affected by the geomorphological feature. Local richness is most probable limited solely by a sampling process of the regional pool, and sample size is determined by factors affecting all species equally, in other words, affect the number of individuals of all species.

1. INTRODUCTION

Atlantic Forest is included in a context of high human interference. Today it is restricted to 7.6% of its original size due to massive deforestation (Morellato & Haddad, 2000). As human activities continue to drive global environmental degradation at an unprecedented speed and scale, biologists are focusing their research efforts on determining the proximate drivers of species diversity. Doing so, it is expected to identify ways of assuring biological conservation and restoration of degraded habitat. There has been a boost towards testing explicit mechanistic hypotheses that evaluate the correlation of diversity with environmental variables, so as to identify environmental drivers of biodiversity (Condamine *et. al.* 2012, Tscharntke *et. al.* 2012).

Ecological theory predicts several mechanisms that might drive diversity. Local diversity is the result of processes occurring at different spatial scales: ecological interactions, such as competition and predation, are predominant at local level, while historical and evolutionary processes prevail at regional scale (Schluter & Ricklefs, 1993). One way to assess processes on a regional scale is comparing geographic regions with different evolutionary histories (Cadle & Greene, 1993), which requires large-scale geographic sampling. An alternative way is to compare adjacent habitats with different evolutionary histories (Soares, 2002), for instance, comparing distinct geomorphological features, which have undergone different processes of soil genesis, and has different times of existence (Ross, 2000).

The processes of soil genesis influence the floristic composition and physiognomy, when generating soils with different properties, providing resources and conditions for different plant species (Huggett, 1995; Ross, 2000). For example, soils of steep slopes drain well and favor water runoff (Karmann, 2000), which can lead to water stress for plants in such slopes. On the other hand, the runoff water can saturate soils of low reliefs and carries metabolic important ions, affecting plant physiology. Water stress may result in the production of lower palatability leaves, reducing their nutritional quality and affecting feeding preferences of primary consumers and influencing all trophic levels of the system (Coley *et al*., 1985). Plants with high nutrient availability and under high light availability are supposed to invest more in growth and reproduction than in the production of chemical defenses (Herms & Mattson, 1992), which would result in more resources for all organisms involved in the trophic web.

Greater resource availability allows increased population size, which reduces extinction probability of a population (Begon *et al*., 2006). A greater abundance of individuals increases the chances of sampling more species.

Despite the bewildering variety of potential diversity drivers, some attempts to synthesize them into unifying schemes may prove fruitful. One of them is Hubbell's (2001) neutral theory of biodiversity. It explains species diversity resulting from a provisionary equilibrium among demographic stochasticity, speciation and dispersion. On local scale, Scheiner and Willig (2005) proposed a unified theory to explain diversity gradients, from which the first two propositions are particularly relevant for this study: (i) variation in environmental factors affects the number of individuals, and (ii) given a uniform environment, with fixed area, more individuals leads to more species. The latter corresponds to the passive sampling or random placement (Coleman,

1981) process that explains diversity increase with increase in number of individuals in an homogeneous area. With random placement of the individuals, we consider it the most parsimonious explanation for diversity variation. Although several studies have discussed the relationship of diversity with number of individuals, their main focus is on the comparison of datasets with different sampling effort (Gotelli & Collwell, 2001), or the estimation of total number of species in the sampled universe (Beck & Schwanghart, 2010).

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(Gangwere, 1961), and may represent shelter from predation. The space in the litter may form different microhabitats for crickets, reducing interspecific competition.

In the litter fauna of crickets predominate micropterous or wingless species (Sperber *et al.*, 2003). Since flight inability restrict crickets to ground level and may limit movement between adjacent sites, their responses may differ between adjacent sites with different geomorphology.

This study investigates drivers of the diversity and abundance of litter crickets, and their possible interactions with geomorphology. We propose an analytical approach which includes local passive sampling as a necessary explanation for diversity variation and thus highlights eventual effects of environmental drivers diversity-abundance relationship.

2. OBJECTIVES

The main objective of this study was to evaluate environmental drivers of abundance and species richness of forest litter crickets. We assumed that the abundance and species richness vary among sites with different geomorphological features. Considering the three distinct geomorphological features in the studied area (Mello, 1997; Meis & Tundisi, 1986), we expected that in the Ancient Streambed, there would be a larger number of cricket individuals and species, followed by Crest, and lowest in Ramps. To explain the assumptions, we suggest some explanatory hypotheses:

Hypothesis 1: The abundance of crickets increases with food resource availability, represented by litter weight.

Hypothesis 2: The abundance of crickets increases with shelter availability, represented by litter depth.

Hypothesis 3 or Biological Neutral Hypothesis: Crickets species richness increases with number of individuals. The idea behind this hypothesis is that the biological processes regulating number of species are not directly affected by the environmental driver. Local species richness would be a sample of the regional species pool, determined by regional-scale evolutionary processes. Local richness would be locally limited solely by a sampling process of the regional pool, and sample size is determined by factors affecting all species equally, i.e., affect the number of individuals.

Hypothesis 4: Cricket species richness is affected both by passive sampling and geomorphological feature, leading to an interaction of number of individuals and geomorphological feature on cricket species richness.

3. MATERIAL AND METHODS

Study Area

Samples were collected in January 07th and 15th, 2005 (Table 1), at the Parque Estadual do Rio Doce (Park, Fig.1). This park is the largest Atlantic forest remnant (semideciduous forest) in Minas Gerais state, with an area of 35,976 ha (IEF 1994), covering the municipalities of Marliéria, Timóteo and Dionísio. The altitude varies between 230 and 515 m (SOCT, 1981).

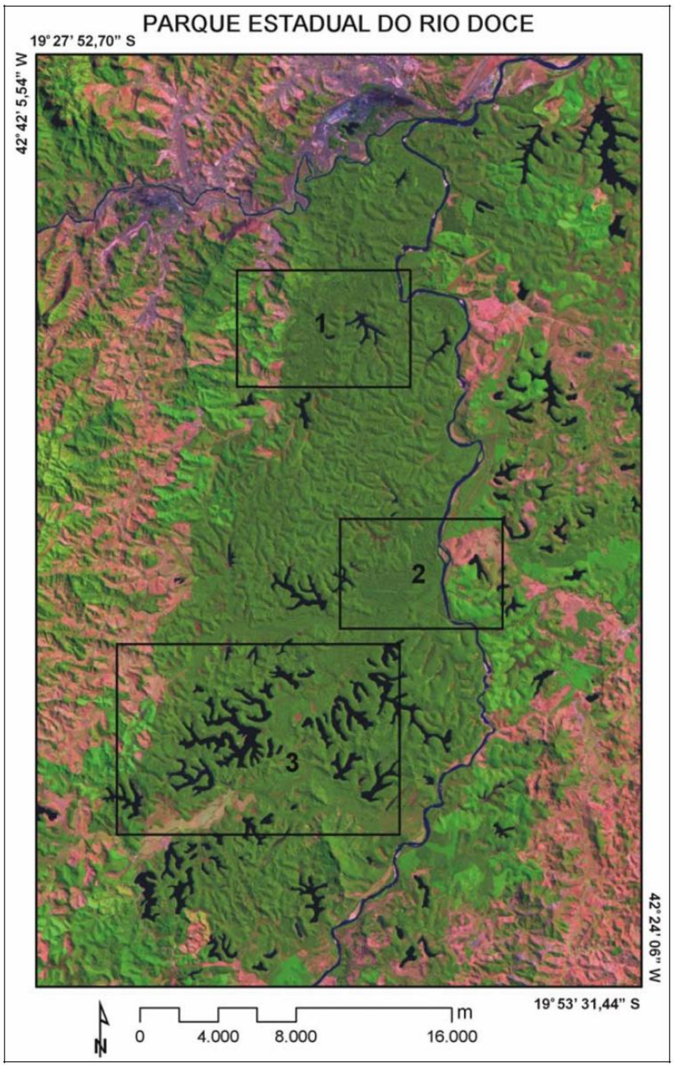

Figure 1. Satellite image of the study area. TMLANDSAT:5R4G3B. Orbit /Point: 217/74-Acquisition 22/08/1997. (1) Area of *Macuco*, (2) Area of *Tereza* trail, (3) Areaof *Gambá*.

The Park has three distinct geomorphological features (Mello, 1997; Meis & Tundisi, 1986): interfluvial domain with eluvial soil (Crest), areas of colluvial slope, which present moved soil, responsible for the barrage of fluvial channels currently occupied by lakes (Ramp) and areas of eluvial plain on the old bed of the Rio Doce river and some of its affluents (Ancient Streambed) (Fig. 2).

The samples covered these three geomorphological features (Soares, 2006) in six different locations (Figs. 2 to 5). Of these six sites, two were in hill Crest feature (Crest of *Macuco* and Crest of *Gambá*), two were in forests located on colluvial Ramp (Ramp of *Macuco* and Ramp of *Gambá*), and two were in the Ancient Streambed (*Tereza*, Table 1). More details on site selection and mapping are available in Soares (2006).

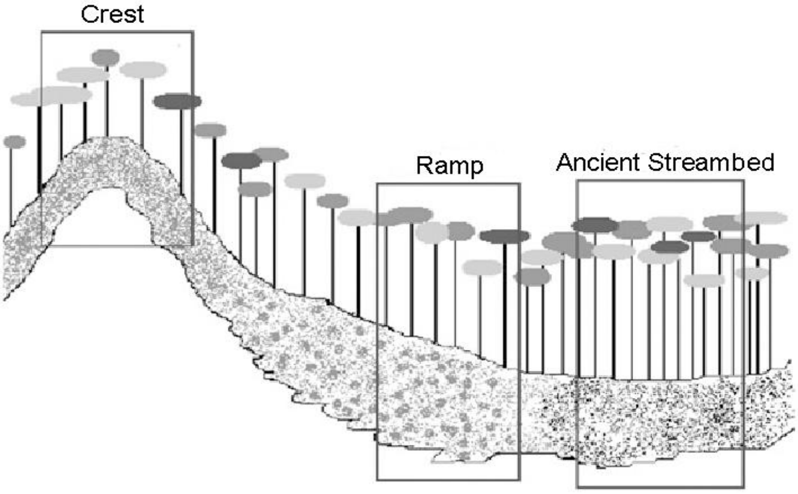

Figure 2. Geomorphological features: interfluve region (Crest), colluvial slope (Ramp) and Ancient Streambed.

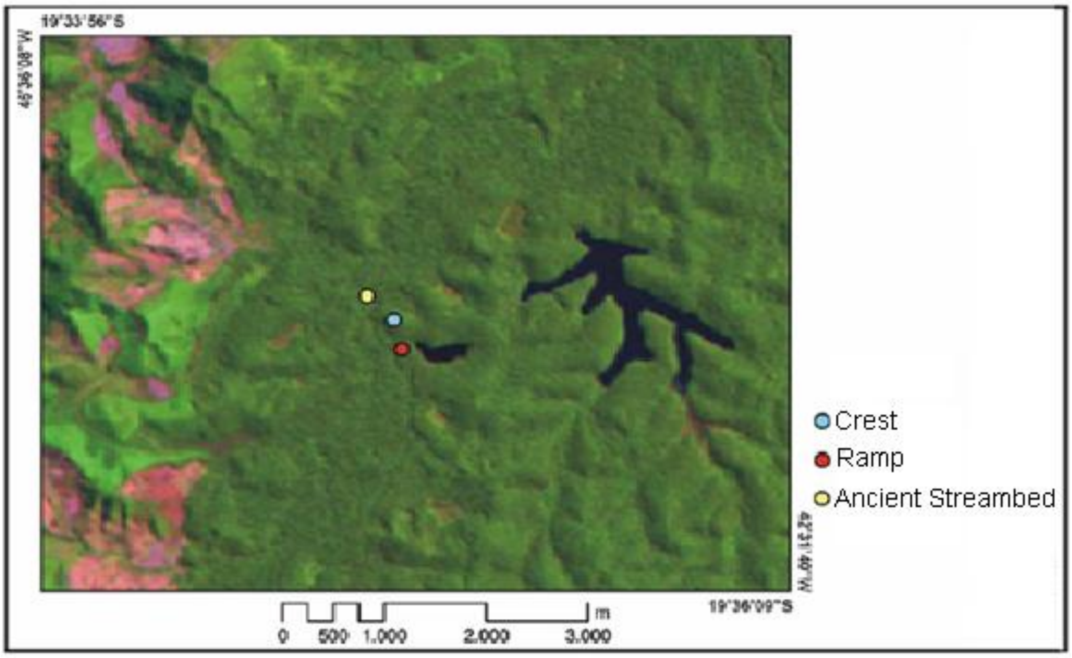

Figure 3. Satellite image of area of *Macuco* (rectangle 1 of figure 1) - indicating the geomorphological features present in this portion. TMLANDSAT: 5R4G3B. Orbit /Point: 217/74 - Acquisition 22/08/1997.

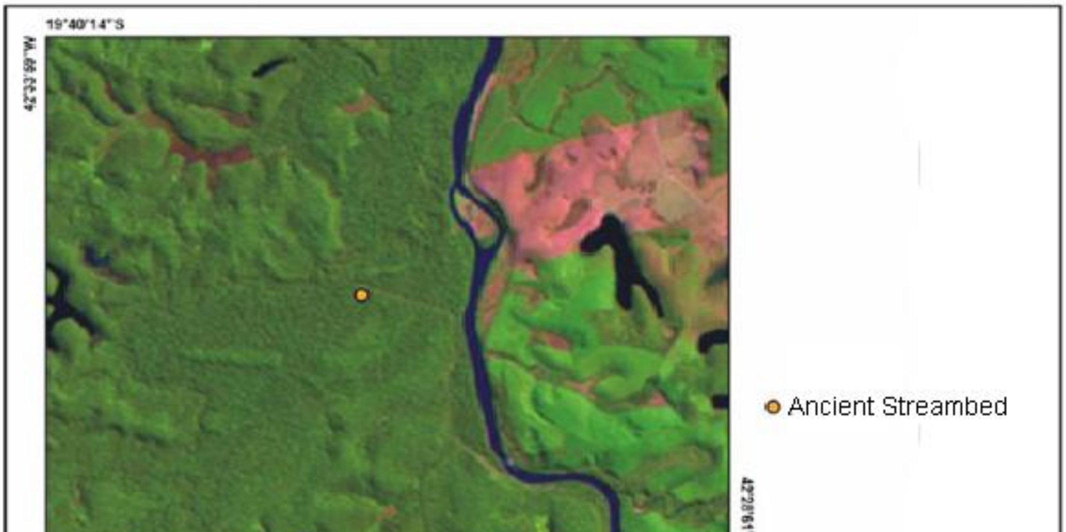

Figure 4. Satellite image of area of Trail of *Tereza* (rectangle 2 of figure 1) - indicating the geomorphological feature present in this portion. TMLANDSAT: 5R4G3B. Orbit / Point: 217/74 – Acquisition 22/08/1997.

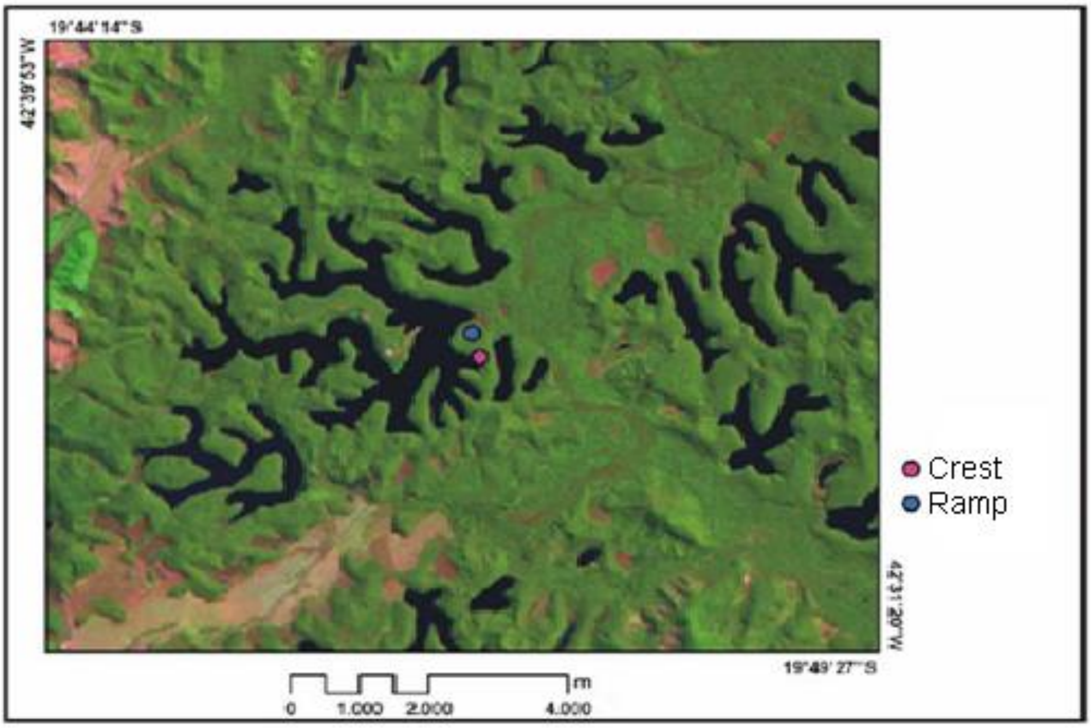

Figure 5. Satellite image of area of *Gambá* (rectangle 3 of figure 1) - indicating the geomorphological features present in this portion. TMLANDSAT: 5R4G3B. Orbit / Point: 217/74 – Acquisition 22/08/1997.

Field Methodology

In each of the six chosen areas, we selected five groups composed by four nearby trees distant 25 meters from each other (Fig. 6, Table 1). Below each of these trees sets a grid (n = 30) was made where nine pitfall traps were buried without the use of bait (Fig. 6), 1m distance between each other and containing a 5% formaldehyde solution. The use of pitfall traps in this work is justified by its greater effectiveness in collecting active animals at ground level (Parsifka *et al.*, 2007), particularly crickets (Sperber et. al., 2003). Overall, 45 traps were set in each area, totaling 270 traps throughout the study. Traps were left in the field for four days.

Beside each grid, a 1 meter square of litter was collected for its weighing, after collecting pitfall traps. Three spots into the grid were arbitrarily selected for the measurement of litter depth using a rule.

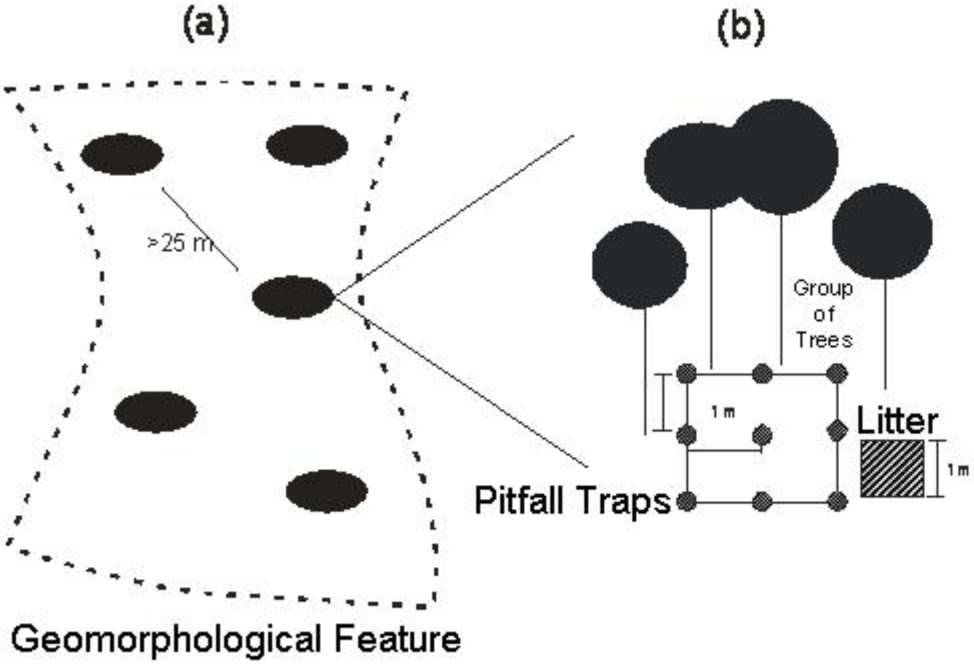

Figure 6. Methodology design. (a)Five groups of trees within the geomorphological feature and (b) grid of pitfall traps beneath each group of trees.

Table 1. Sampled areas with their features, geographical coordinates and dates of sampling.

Areas	Geomorphological Feature	Geographic Coordinates	Dates of sampling
Macuco	Crest	19º35'24.04" S 42º33'41.44" O	12/1/2005

Macuco	Ramp	19º35'31.75" S 42º33'43.07" O	12/1/2005
Macuco	Ancient Streambed	19º35'19.63" S 42º33'43.60" O	12/1/2005
Gambá	Crest	19º47'07.00" S 42º35'10.73" O	14/1/2005
Gambá	Ramp	19º46'39.81" S 42º35'19.46" O	14/1/2005
Tereza	Ancient Streambed	19º42'09.22" S 42º35'19.46" O	14/1/2005

Laboratorial Methodology

Crickets were identified until lowest possible taxonomic level and then stored in the Laboratório de Orthoptera's (DBG) collection, filliated to the Museu de Entomologia of Universidade Federal de Viçosa (UFVB).

Analytical Approach

We propose that, to test the effects of potential environmental drivers upon diversity, a statistical model is used that not only includes the potential environmental driver as an explanatory variable, but also the accumulated number of individuals in each sample, and their interaction term. If only accumulated abundance affects diversity, then variation in species richness among sampling units would result exclusively from a neutral biological sampling effect: that is, sites with more individuals have more species because they offer a larger proportion of the sampling universe.

A significant effect of the interaction term indicates evidence for an effect of the environmental driver upon species number accumulation number of individuals. In this case, the driver changes the species-abundance relationship of the ecological community.

If there was a direct effect of the environmental driver on species co-ocurrence (e.g. niche partitioning), we expect a significance for the effect of the driver on diversity.

Diversity was estimated as species counts. We opted to avoid the use of species richness estimators (Beck & Schwanghart, 2010), because we were interested in the diversity-abundance relationship and its eventual response to environmental variables. Abundance was the accumulated number of individuals of all species in each sample. We used logarithm of abundance in model fitting, in order to follow the theoretical models relating biodiversity with abundance (Preston, 1962; Hubbell, 2001).

To evaluate if our approach changed the interpretation of environmental effects on diversity, we performed analyses of the environmental variable as single explanatory variable, and compared these with analyses using the environmental variable as additional explanatory, together with abundance and the interaction term. In all analyses, we adjusted generalized linear models (GLMs) assuming Poisson error distribution (O'Hara & Kotze, 2010), corrected when the dispersion parameter (dp) was < 0.9 or > 1.5. When using Poisson errors, we tested significance by using Chi-squared tests, and whenever over- or under-dispersions had to be corrected, we tested the significance using F test (Crawley, 2007; Logan, 2010). Significance was tested through model comparisons, deleting non-significant explanatory effects. All models were submitted to residual analyses, to check for the suitability of the models and of the error distribution. Drawing of the curves estimated by the minimal adequate models was restricted to the available data ranges (Ribas *et al.*, 2003), so as to avoid undue extrapolation. We considered 5% significance level. All analyses and graphs were done under R (R Development Core Team, 2009).

4. RESULTS

A total of 2046 individuals belonging to 23 species and 6 families were collected (Table 2).

Table 2. Cricket species, their families and abundance by species

Species	**Family**	**Abundance**
Amanayara sp.	Trigonidiidae	183
Anaxipha sp.1	Trigonidiidae	92
Anaxipha sp.2	Trigonidiidae	26
Anaxipha sp.3	Trigonidiidae	4
Brasilodontus sp.	Eneopteridae	113
Cyrtoxipha sp.	Trigonidiidae	1
Ectecous sp.	Phalangopsidae	166
Eidmanacris sp.	Phalangopsidae	41
Eneoptera surinamensis	Eneopteridae	27
Gryllidae gen.	Gryllidae	45
Guabamima sp.	Phalangopsidae	101
Laranda sp.	Phalangopsidae	1
Miogryllus sp.	Gryllidae	38
Mogoplistidae sp. 1	Mogoplistidae	9
Mogoplistidae sp. 2	Mogoplistidae	2
Nemobiinae sp.	Trigonidiidae	2
Neometrypus sp.	Eneopteridae	1
Paragryllinae sp.	Phalangopsidae	3
Podoscirtidae sp.	Podoscirtidae	2
Strogulomorphini sp.	Phalangopsidae	23
Tafalisca sp.	Eneopteridae	6

Trigonidiidae sp.	Trigonidiidae	4
Zuchiella sp.	Trigonidiidae	1137
Not identified	-	19
TOTAL	6 families	2046

The most abundant species was *Zuchiella* sp., representing more than half of the total abundance of crickets. Some individuals could not be identified as they were very young nymphs. The new genus and new species are to be described in further work and are evidence of incipient studies on cricket taxonomy in Brazil.

The distribution of the crickets on each geomorphological feature is displayed on Table 3.

Table 3. Cricket species and their distributions on each geomorphological feature.

Species	**Crest**	**Ramp**	**Ancient Streambed**
Amanayara sp.	48	51	84
Anaxipha sp.1	37	10	45
Anaxipha sp.2	10	1	15
Anaxipha sp.3	0	0	4
Brasilodontus sp.	37	21	55
Cyrtoxipha sp.	0	1	0
Ectecous sp.	38	52	76
Eidmanacris sp.	30	6	5
Eneoptera surinamensis	12	1	14
Gryllidae gen.	20	12	13

Guabamima sp.	22	43	36
Laranda sp.	0	1	0
Miogryllus sp.	2	11	25
Mogoplistidae sp. 1	3	3	3
Mogoplistidae sp. 2	0	2	0
Nemobiinae sp.	0	2	0
Neometrypus sp.	0	0	1
Paragryllinae sp.	1	1	1
Podoscirtidae sp.	0	0	2
Strogulomorphini sp.	5	13	5
Tafalisca sp.	0	5	1
Trigonidiidae sp.	0	2	2
Zuchiella sp.	273	209	655
Not identified	1	4	14
TOTAL	539	451	1056

Testing of Assumptions

The variable geomorphological feature could be amalgamated into two categories, since the categories Crest and Ramp did not differ among themselves as to the number of individuals ($F_{1, 28}$ = 0.097, P = 0.757) and number of species ($F_{1, 28}$ = 0.26, P = 0.613). The abundance responded significantly to the geomorphological feature ($F_{1, 28}$ = 9.12, P = 0.005, Fig. 9), being higher in Ancient Streambed than in Crest + Ramp. Species richness did not differ among geomorphological feature ($F_{1, 28}$ = 3.892, P = 0.058, Fig. 10).

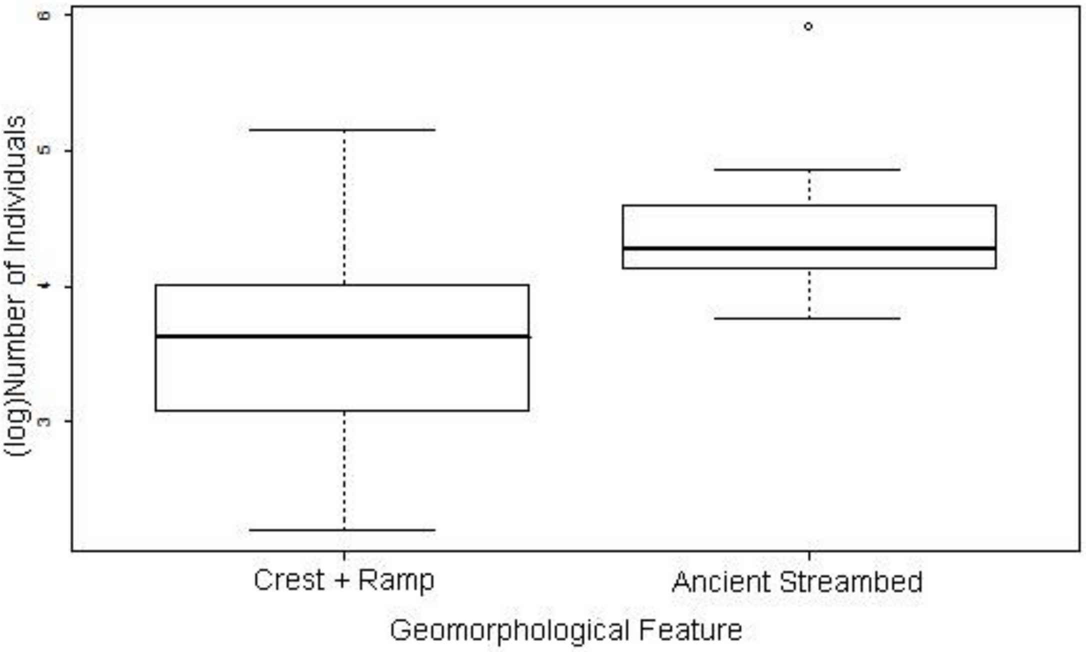

Figure 7: Logarithm of the number of individuals collected from a nine traps set depending on geomorphological features, "Crest+Ramp" and "Ancient Streambed". The box is delimited by first and third quartile and corresponds to 50% of the data. The dark line corresponds to the median and the dotted lines show the minimum and maximum value of the data. $F_{1,28}$=9,1292; P=0,005.

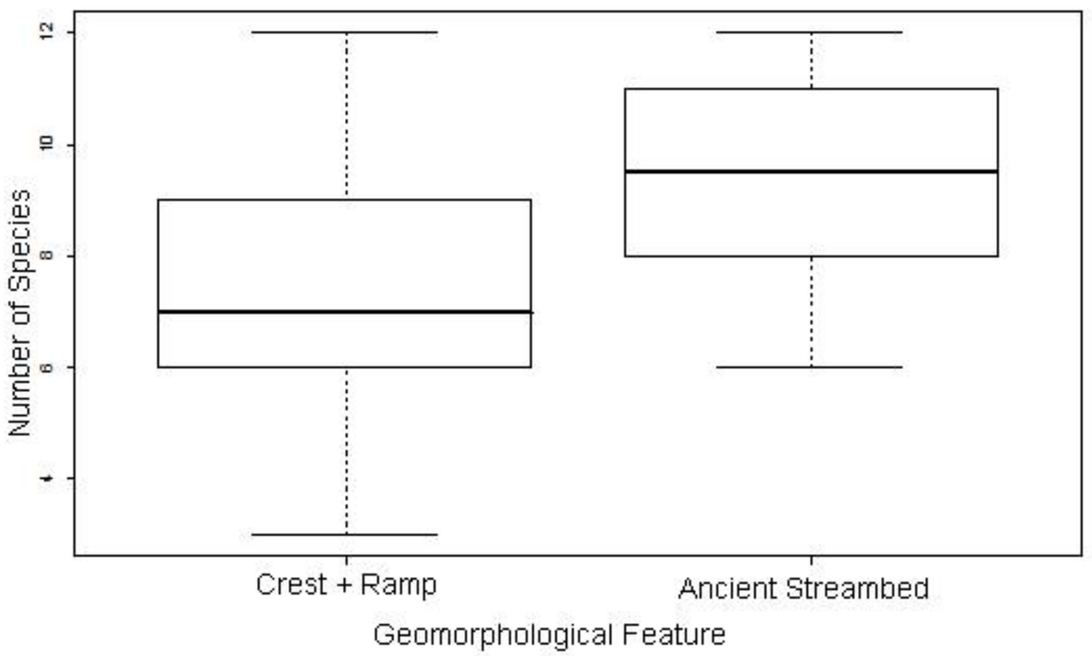

Figure 8: Number of species of crickets from a nine traps set depending on geomorphological features,"Ramp+Crest" and "Ancient Streambed". The box is delimited by first and third quartile and corresponds to 50% of the data. The dark line corresponds to the median and the dotted lines show the minimum and maximum value of the data. $F_{1,28}$=3,892; P=0,058.

Hypotheses 1 and 2 Tests

The abundance itself did not respond significantly to the variables litter weight ($F_{1, 28}$ = 0.497, P = 0.486) and depth ($F_{1, 28}$ = 2.7491, P = 0.108).

Litter weight did not explain the difference in abundance in the geomorphological features ($F_{1, 28}$ = 3.867, P = 0.0596). The litter depth explains significantly ($F_{1, 28}$ = 4.533, P = 0.0425, Fig. 9) the above-mentioned difference.

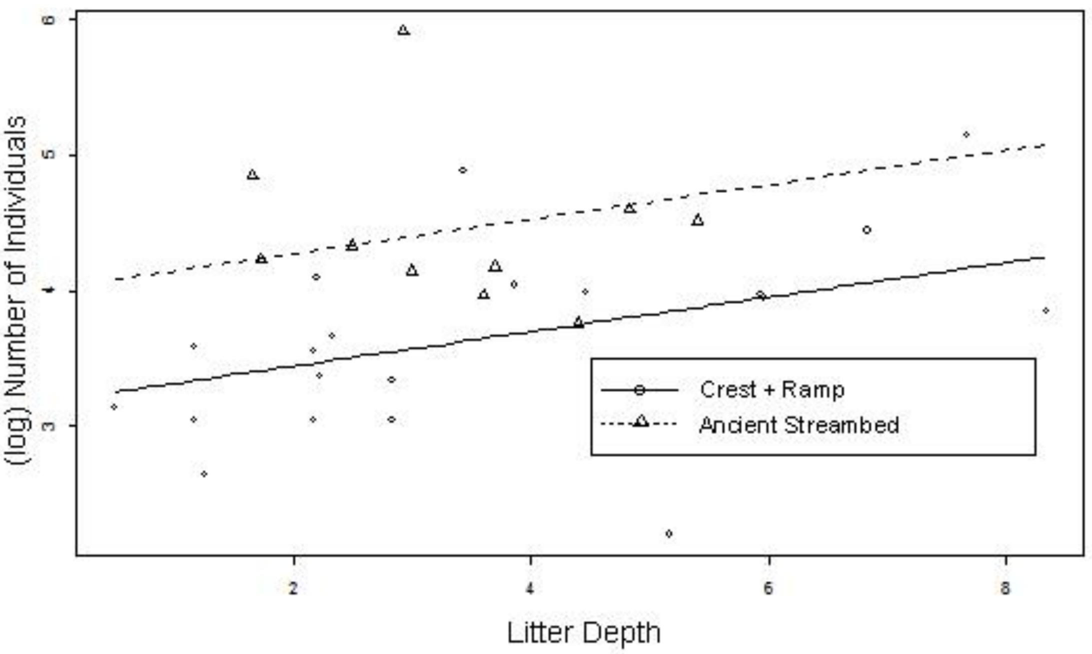

Figure 9: Logarithm of the number of individuals collected from a nine traps set depending on the average depth of litter between the geomorphological features. Continuous line refers to the feature "Ramp+Crest" and the dashed line refers to the feature "Ancient Streambed". $F_{1,28}$=4,533; P=0,0425.

Biological Neutral Hypothesis (Hypothesis 3)

There was a positive correlation between the logarithm of the number of individuals and species richness, which we consider the biological neutral hypothesis ($F_{1,\,28}$ = 14.364, P = 0.000735, Fig. 10).

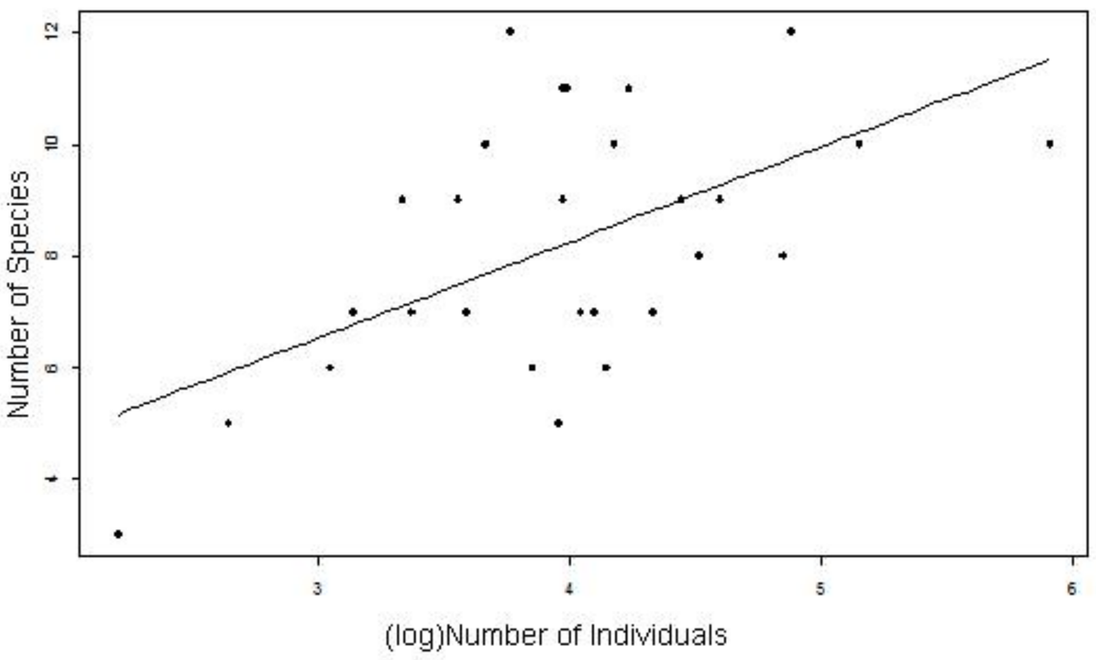

Figure10: Biological Null Hypothesis: Number of species of crickets depending on the logarithm of the number of individuals per nine traps set. F1,28=14,364; P=0,000735.

Hypothesis 4 Test

Using the ANOVA approach, we did not detect any difference of cricket diversity among geomorphological features ($F_{1, 28}$ = 3.892, P = 0.058, Fig. 8). With the ANCOVA approach, on the other hand, we detected a significant interaction of geomorphologic feature with cricket abundance ($F_{1,26}$=7.01; P=0.01, Fig. 11). Whereas on the Crest and Ramp, cricket diversity increased with abundance ($F_{1,18}$=18.51; P=0.0004*)*, diversity was not affected on the Ancient Streambed by the number of individuals in the sample ($F_{1,8}$=0.19; P=0.67). Cricket abundance was lower on the Crest and Ramp than on the Ancient Streambed. The deletion of a single outlier, with more than 350 individuals on Ancient Streambed, did not alter the results.

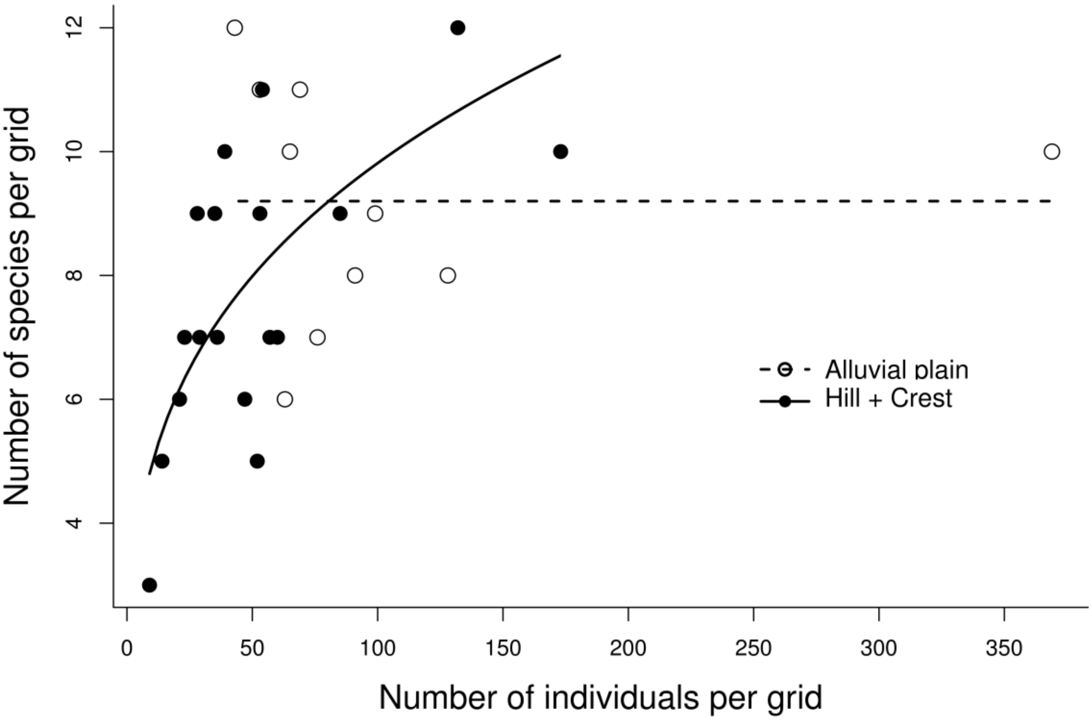

Figure 11: Number of species of crickets depending on the number of individuals collected from a nine traps set among the geomorphological features. Continuous line refers to the feature "Ramp+Crest" and the dashed line refers to the feature" Ancient Streambed ". $F_{1,28}$=3,189, P=0,0577.

5. DISCUSSION

Although the assumption has not been exactly as expected, the general idea is the same: higher abundance in Ancient Streambed. The assumption can be explained taking into account the stability of the Ancient Streambed soil, which can accumulate more litter and provide, therefore, food resources and shelter from predators, ending in a greater number of individuals.

The hypotheses to explain the difference in abundance in the geomorphologic feature were satisfactory: there was a significant result for litter depth, as we wanted to demonstrate, though not significant for weight. The result for weight can be explained by the fact that the variable does not represent enough of the food resource. Heavier litter is not necessarily qualitatively more attractive to litter crickets.

We detected an increase of diversity with accumulated abundance. We suggest that this may result from local passive sampling, where sites with higher densities represent a larger sample of the regional species pool. This effect is analogous to the veil line proposed by Preston (1948). Preston argued that species abundance distribution follows a log-normal (Gaussian) distribution, but that this distribution is often not detected due to insufficient sampling effort. Given that in Preston's log-normal abundance distribution, species toward the left side of the x-axis are increasingly rare, they may be missed in a random species sample. As sample size increases, the likelihood of collecting rare species increases (Green & Young, 1993), and more of the normal distribution becomes visible (Magurran, 2004). The sample size determined by factors that affect all species equally, ie, affect the number of individuals.

We propose that the abundance effect of local passive sampling should be considered as a biological neutral explanation for local diversity variation. It is more parsimonious to consider effects of environmental drivers on the whole accumulated abundance, with diversity as a mere sampling effect of abundance differences, than to consider that environmental drivers affect the diversity directly. Explaining diversity as resulting from passive sampling implicates in considering all species as biologically equivalent, sharing the same environmental needs, as in Hubbell's Neutral Theory (Hubbell, 2001). Any effect on diversity, without taking accumulated abundance into account, has the implicit assumption that species are different in their environmental needs. This explanation should only be invoked when we have strong evidence that discards simpler explanations. This is an extension of the Principle of Parsimony (Occam's razor) (Blumer et al., 1987), so valuable for the development of science (Crawley, 2007). If local diversity is determined solely by passive sampling effects, without any interaction among the components of the system – the individuals – local diversity should correlate exclusively with accumulated abundance in the sample. In this case, no variation in diversity should be explained by other effects.

The “abundance as co-variable” approach changed qualitatively the interpretation of the effects of the environment, highlighting hidden environmental effects. The “usual” approach would lead to rejection of environmental drivers of biodiversity. Biologically still more relevant is that the interactions detected by the “abundance as co-variable” highlight changes in the abundance distributions, driven by the environment, that may be linked to emergent properties of these communities.

The geomorphological feature regulates the richness as follows: in Ancient Streambed, even when the number of individuals is high, richness remains. That would be a sign of a community saturated in that feature. On the Crest and Ramp, there are a greater number of species in greater abundance. This increase is logarithmic, which adequately represents the line of the veil, which means rare species are more easily detected when the sampling site is increased.

6. CONCLUSION

The biological processes regulating number of species are not directly affected by the geomorphological feature. Local richness is most probable locally limited solely by a sampling process of the regional pool, and sample size is determined by factors affecting all species equally, in other words, affect the number of individuals.

The analytical approach we propose here highlights potential mechanisms capable of explaining empirically observed responses of species diversity to environmental drivers, and generates novel insights that cannot be obtained from previous empirical studies.

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UNIVERSIDADE FEDERAL DE VIÇOSA
POSTGRADUATE PROGRAMME IN ENTOMOLOGY

CHAPTER TWO

Why are there more species in some taxa than in others?

Master Dissertation

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2012

ABSTRACT

Assuming monophyly, the number of species per genus may result from differential evolutionary age and differential diversification rates. Biological characteristics of the organisms may affect diversification. Increasing body size may reduce habitat fractal perception of the organisms, reducing speciation or species co-occurrence. Distribution area of the genus may represent an abiotic diversity driver as well as a consequence of biological processes. Area may correlate to evolutionary age and diversification probability. There may be, however, sampling effects, related to research intensity bias, which interfere with observed diversity patterns. For example, recorded distribution area may result from research intensity, and large-body genera may be more easily collected. Here we aimed to evaluate if genus diversity of South-American crickets (Orthoptera: Grylloidea) may be empirically explained by distribution area and mean body size. We expected that diversity would correlate positively with area and negatively with body size. We analyzed all species reported in the Orthoptera Species File with geographic distribution range reported for the Neotropics, counting number of extant species per genus. We estimated reported distribution area, as well as intercepted biome area for each genus. Body size was estimated by the median hind femur length. We adjusted generalized linear models with Poisson errors, corrected for overdispersion when necessary, with species per genus as response variable, and body size, distribution area and their interaction term as explanatory variables. As far as some reported areas were discontinuous, we included this information as a categorical explanatory variable in the models (ANCOVA). Among the 329 species, in 92 genera, recorded, we considered 242 species, of 89 genera, because of lack of body size data for two genera and one outlier (*Uvaroviella*).

There was an interaction of area continuity with accumulated distribution area ($\chi^2_{1,85}$=5.49; p=0.019): diversity increased with area ($\chi^2_{1,87}$= 73.63; $p < 0.0001$), but this increase was higher and steeper in discontinuous than continuous areas ($\chi^2_{1,86}$= 43.21; $p < 0.0001$). Diversity increased with body and area in both continuous (body: $\chi^2_{1,72}$= 25.99; $p < 0.0001$; area: $\chi^2_{1,72}$= 21.71; $p < 0.0001$) and discontinuous (body: $F_{1,13}$= 5.39; p = 0.037; area: $F_{1,13}$= 22.64; p = 0.00037) distribution areas. Discontinuous distribution records may either underestimate actual distribution area, or overestimate the genus scope. Genera with discontinuous records may amalgamate more than one actual genus. As our data were restricted to one geographical area (South America), we consider that sampling effort was comparatively homogeneous, reducing the eventual effect of researcher effort differences among genera. Therefore, biological processes are a more suitable explanation for the detected area effects. The increase of diversity with body size was opposite to our expectations. This could result from sampling effect, where larger cricket species with smaller body size would be under-represented due to taxonomic issues. We conclude that cricket distribution data, although sparse and not-systematic, are relevant to explain species diversity among genera. The biological processes involved in the empirical relationships deserve further investigation.

1. INTRODUCTION

May (2010) has proposed that if aliens visited our planet and asked “How many distinct life forms – species – does your planet have?”,we would be “embarrassed” by the uncertainty in our answer. In fact, if this alien asks an ecologist, the answer would most likely to be “Why do you want to know?”. There are plenty of reasons that justify us to know how many species are there in a location. First of them, the ethical reason: each species has a value in itself, therefore all of them are important; knowing the number would be important because of the simple fact that they exist and must be known. Knowing how many species are there may also justify conservation of areas, including one of the most trending topics in ecology: functioning of ecosystem, although many may agree that number of species is not the most suitable measure when it comes to conservationism.

May (1988) has already tried to estimate world species number based on size of organisms, premising that larger individuals would be less abundant. However, further studies confirmed different modes of evolution among small species and inconsistent body size frequency distributions among taxa (Gaston & Blackburn 2000).

Some taxonomic patterns may also have been taken into account, like time-species accumulation curves and author-species accumulation curves. These taxonomic patterns may have limitations related to the concept of species and to the fact that different taxonomic communities may have different levels of differentiation. Any increase or decrease on higher taxa may have an effect on any method of prediction of species. These changes may be caused by new taxa discovered, division or grouping due to filogenetic studies or by detection of synonyms.

One of the strongest determinants of species discovery rates may be taxonomic effort. Though the discovery rate on higher taxa may be lowering, the rate of description of new species remains relatively constant, suggesting that there is at least sufficient effort to describe new species at a constant rate. Also, despite decreasing number of taxonomic experts, other factors, such as more amateur taxonomists and phylogeneticists, new sampling methods and molecular identification tools and better access to information, are counteracting this trend (Mora et. al. 2011).

As shown above, knowing how many species are there is a challenging question by itself. Knowing how the predictions have been made may give us clues to figure out what are the real drivers of diversity. Moreover, it can be useful to realize what may be fundamental in speciation or extinction processes. Using a why question, such as “Why are there more species in some taxa than in others?”, give us the possibility of discussing mechanisms that lead to diversity.

In a bewildering diversity of organisms, some genera are way more diverse than others. Grylloidea is not an exception. For example, while *Acantoluzarida* is a monospecific genus (*Acantoluzarida nigra* Desutter-Grandcolas), *Gryllus* has 93 described species.

Assuming all the species in a genus share the same unique ancestral, several theoretical hypothesis will be presented to answer the title why question. This hypothesis are displayed as a flowchart at Figure 1.

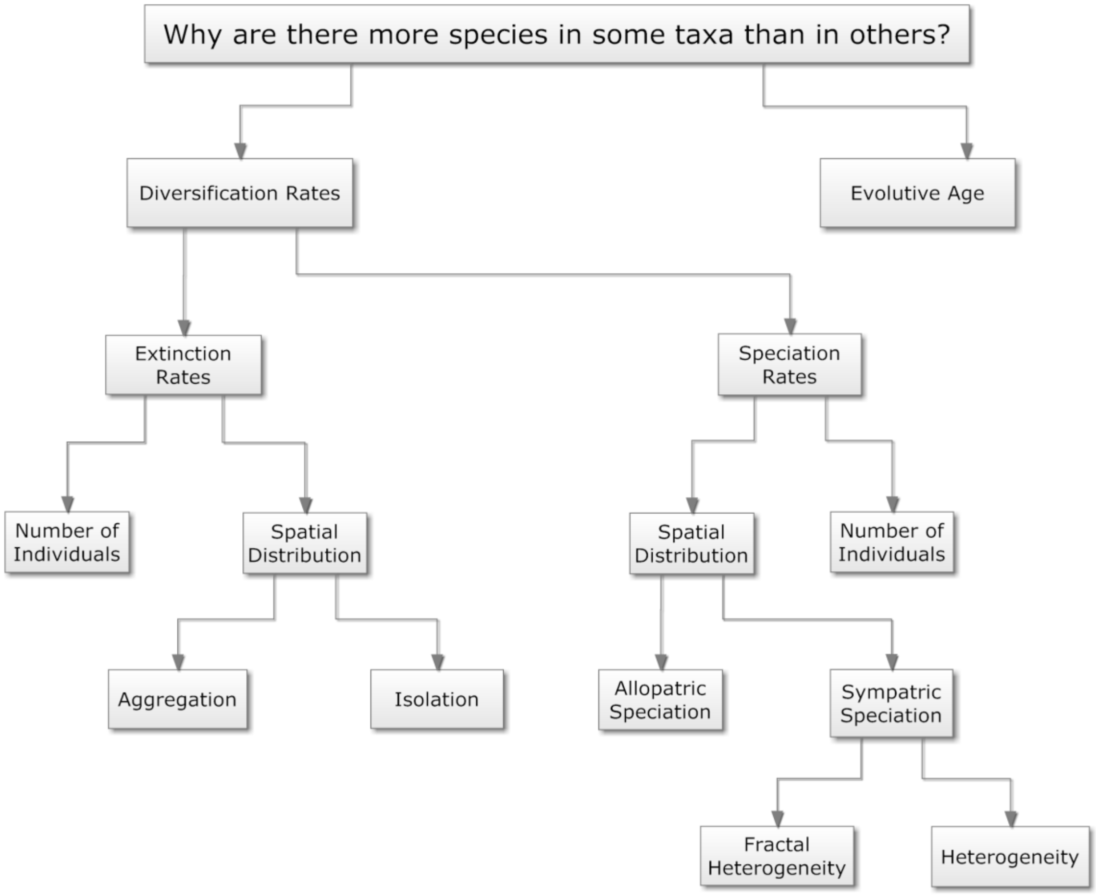

Figure 1: Flowchart of theoretical hypoteses that may answer “Why are there more species in some taxa than in others?”

Hypothesis 1: Evolutive age. Considering equal speciation and extinction rates among all genera, and considering speciation to be higher than extinction rates, one shall have more species if there was more time to occur speciation. In other words, one genus is more diverse than other because of accumulated diversification time.

Hypothesis 2: Diversification rates. Alternatively to hypothesis 1, we shall consider different speciation and extinction rates among genera. In this context, even same-aged genera may have differences between its numbers of species.

Hypothesis 2.1: Speciation rates. One genus has a higher speciation rate than another, leading to a higher number of species.

Hypothesis 2.1.1: Number of individuals. Considering speciation an event that is more probable to occur when there is a higher number of organisms, analogously to point mutation, an increased number of individuals would make speciation chance higher. Hubbel's neutrality model predicts such correlation. (Hubbell 2001; Rosindell et. al. 2011)

Hypothesis 2.1.2: Spatial distribution. Space is strongly related to events of speciation. Traditionally, the main process that leads to speciation is allopatric. Sympatric speciation, though polemic and hotly contested, is also a theoretical alternative.

Hypothesis 2.1.2.1: Allopatric speciation. This include species undergoing genotypic and/or phenotypic divergence as they become subjected to different selective pressures and independently undergo genetic drift, with different mutations arising in the populations' gene pools. (Hoskin et.al. 2005)

Hypothesis 2.1.2.2: Sympatric speciation. Speciation events occur while species inhabiting the same geographic region.

Hypothesis 2.1.2.2.1: Fractal Heterogeneity. A grassland may be homogeneous to a cow, but an insect may be able to find differences within each leaf. In other words, the smallest the organisms, more heterogeneous the environment becomes, higher the chance to speciate. (Morse et al 1985)

Hypothesis 2.1.2.2.2: Heterogeneity *per se*. Specialization. Heterogeneity itself may increase speciation rates (Cowling & Lombard 2002).

Hypothesis 2.2: Extinction rates. In an analogous manner, genera with higher extinction rates should have less species.

Hypothesis 2.2.1: Number of individuals. Analogously to speciation, the lower the number of individuals, the higher the chance of extinction of the species. This may be explained by a strong Allee effect or even by Hubbell's neutrality model.

Hypothesis 2.2.2: Spatial distribution. How organisms are distributed in the environment may have effect in the persistence of the species. Either isolation or aggregation of individuals may lead to extinction.

Hypothesis 2.2.2.1: Isolation. When organisms are too far away from each other, the species may be endangered by low meeting rates between males and females. When populations are spare, the rescue effect can be compromised, leading to extinction.

Hypothesis 2.2.2.2: Aggregation. Organisms that are too close from each other may have restrict geographic range, making the species more susceptible to local catastrophes.

These are theoretical hypothesis. At this study we focused on testing if genus diversity of crickets may be empirically explained by distribution area and mean body size, which would be an indirect measure of overall abundance.

2. OBJECTIVES

Considering the comprehensive question “Why are there more species in some taxa than in others?” and all the theoretical hypotheses that may answer it, we aimed to evaluate if genus diversity of South-American crickets (Orthoptera: Grylloidea) may be empirically explained by distribution area and mean body size. We expected that diversity would correlate positively with area and negatively with body size.

3. METHODOLOGY

We analyzed all species reported in the Orthoptera Species File (OSF) with geographic distribution range reported for the Neotropics, counting number of extant species per genus. Species that occur both on South and Central America were included to fulfill the criteria involving continuous biome. Species exclusively reported to Central America and/or islands were not considered.

We searched each of the species description mentioned above for their hind femur length. When, in the species description, the author measured more than one individual, we used the median so as to have an estimate independent of the sample size. Also, we used the median of hind femur lengths of all species belonging to a genus to determinate the measure for this genus. All measures were taken in millimeters.

Geographic range was based on records in the Orthoptera Species File (OSF). We estimated reported distribution area, as well as intercepted biome area for each genus, using data from Olson *et. al.* (2001). We used several criteria to set distribution, as followed:

1. Political area of the country(ies) or region(s), as reported in OSF. Brazil and Argentina were most often subdivided in geographical regions.

2. Minimum Continuous Biome (MCB): Tropical, subtropical moist broadleaf forest (subdivided in the following groups: Amazonian, Atlantic and Andean) and, specifically for *Neogryllodes*, which is not recorded for forested area, we used the area of patagonian grasslands. To clarify these criteria, we presented an example:

– If a species is reported for Amazon and Northeast of Brazil, the MCB equals the area of Amazonian forest.

– If a species is reported for Southeast and Northeast of Brazil, the MCB equals the area of Amazonian forest plus the area of Atlantic forest, because the reported areas intercept both biomes.

- If a species is reported for Amazon and Southeast of Brazil, the MCB equals the area of Amazonian group plus the area of Atlantic group.

- If a species is reported for “Brazil”, with no records of the political region, but the study is known to be run in a biome, as Saussure (1874), the MCB equals the area of the biome where the study took place (on this case, Amazonian group).

3. Continuous Forest (CF): Tropical, subtropical moist and dry broadleaf forest (subdivided on the following groups: Amazonian and Atlantic).

4. Minimum Continuous Alternative Biome (MCAB): continuous coverage of an alternative biome, intercepted by the record area of the genus.

We tested which of the four criteria for geographic distribution would be the best estimative of area. In other words, which criteria would have a significant relationship with number of species per genus.

All analyses and graphs were done under R (R Development Core Team 2009). We considered 5% significance level. In all analyses, we adjusted generalized linear models (GLMs) assuming Poisson error distribution (O'Hara & Kotze 2010), corrected when the dispersion parameter (dp) was < 0.9 or > 1.5. When using Poisson errors, we tested significance by using Chi-squared tests, and whenever over- or under-dispersions had to be corrected, we tested the significance using F test (Crawley 2007; Logan 2010). We set species per genus as response variable, and body size, distribution area and their interaction term as explanatory variables. As some reported areas were discontinuous, we included this information as a further categorical explanatory variable in the models (ANCOVA). All models were submitted to residual analyses, to check for the suitability of the models and of the error distribution.

4. RESULTS

A total of 329 species were considered, among 92 genera. We descarded unmeasured or mutilated holotypes, we worked with 90 genera and 301 species. *Uvaroviella* was considered an outlier, with 59 species described, most of them recently by the same author (Otte 2006, Otte & Perez Gelabert 2009).

There was an interaction of area continuity with accumulated distribution area ($\chi^2_{1,85}=5.49$; $p=0.019$; Fig. 2): diversity increased with area ($\chi^2_{1,87}= 73.63$; $p < 0.0001$), but this increase was higher and steeper in discontinuous than continuous areas ($\chi^2_{1,86}= 43.21$; $p < 0.0001$).

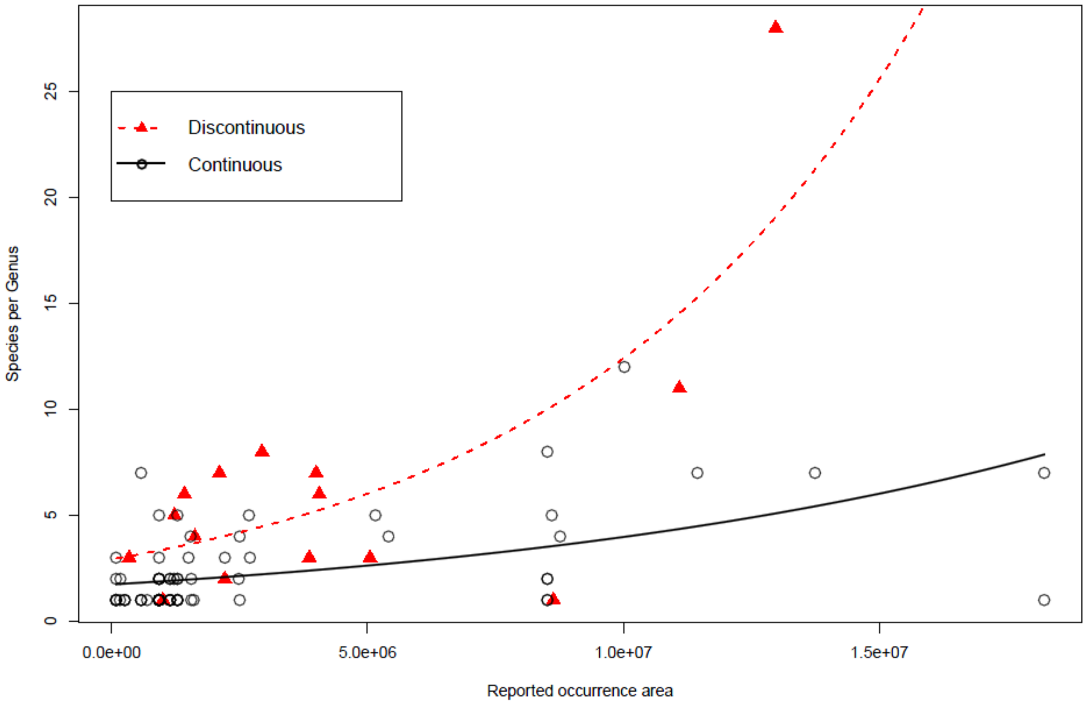

Figure 2: Interaction of area continuity with reported occurrence area ($\chi^2_{1,85}=5.49$; $p=0.019$): Species per genus increased with area ($\chi^2_{1,87}= 73.63$; $p < 0.0001$), but this increase was higher and steeper in discontinuous than continuous areas ($\chi^2_{1,86}= 43.21$; $p < 0.0001$).

Diversity increased with body size and area in both continuous (body, Fig. 3: $\chi^2_{1,72} = 25.99$; $p < 0.0001$; area, Fig. 4: $\chi^2_{1,72} = 21.71$; $p < 0.0001$) and discontinuous (body, Fig. 5: $F_{1,13} = 5.39$; $p = 0.037$; area, Fig. 6: $F_{1,13} = 22.64$; $p = 0.00037$) distribution areas.

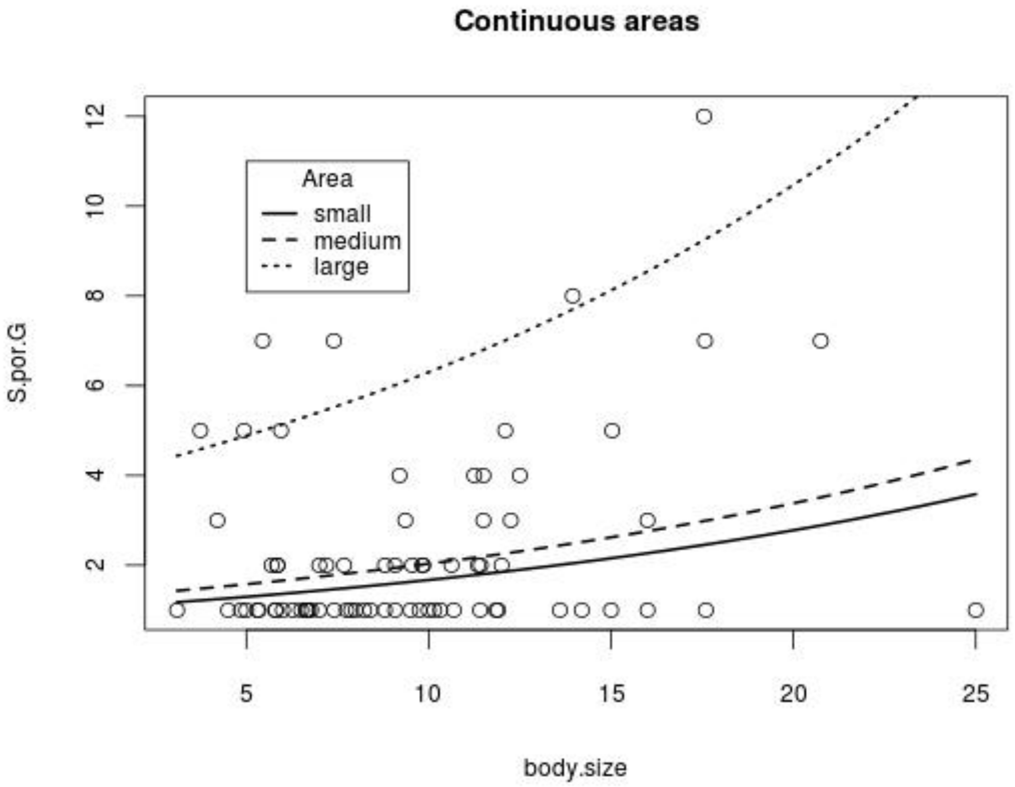

Figure 3: Species per genus increased with body size in continuous distribution areas: $\chi^2_{1,72}$= 25.99; p < 0.0001

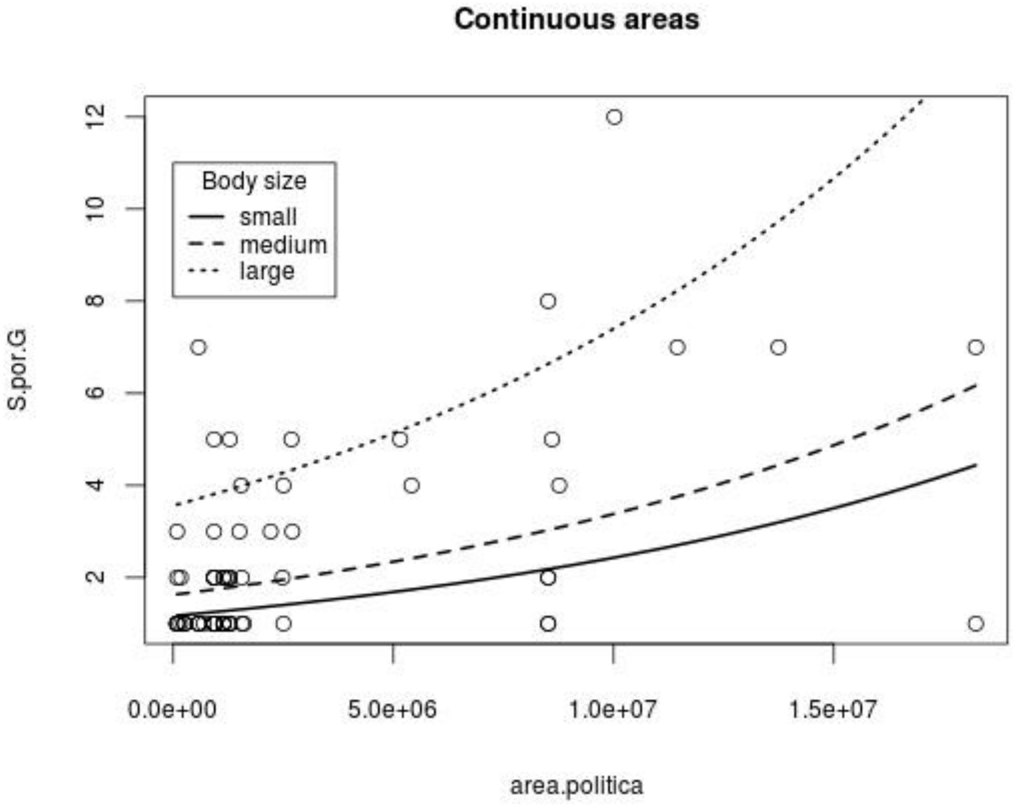

Figure 4: Species per genus increased with reported occurrence area in continuous areas: $\chi^2_{1,72}$= 21.71; $p < 0.0001$

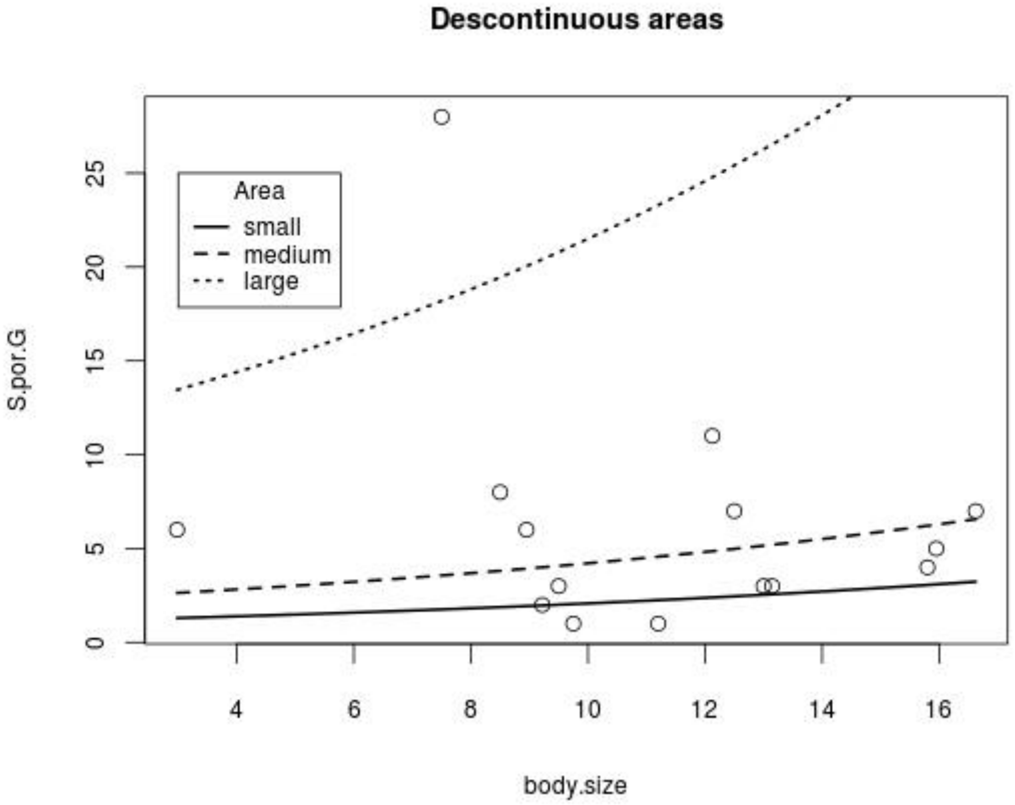

Figure 5: Species per genus increase with body size in descontinuous areas: F $_{1,13}$= 5.39; p = 0.037

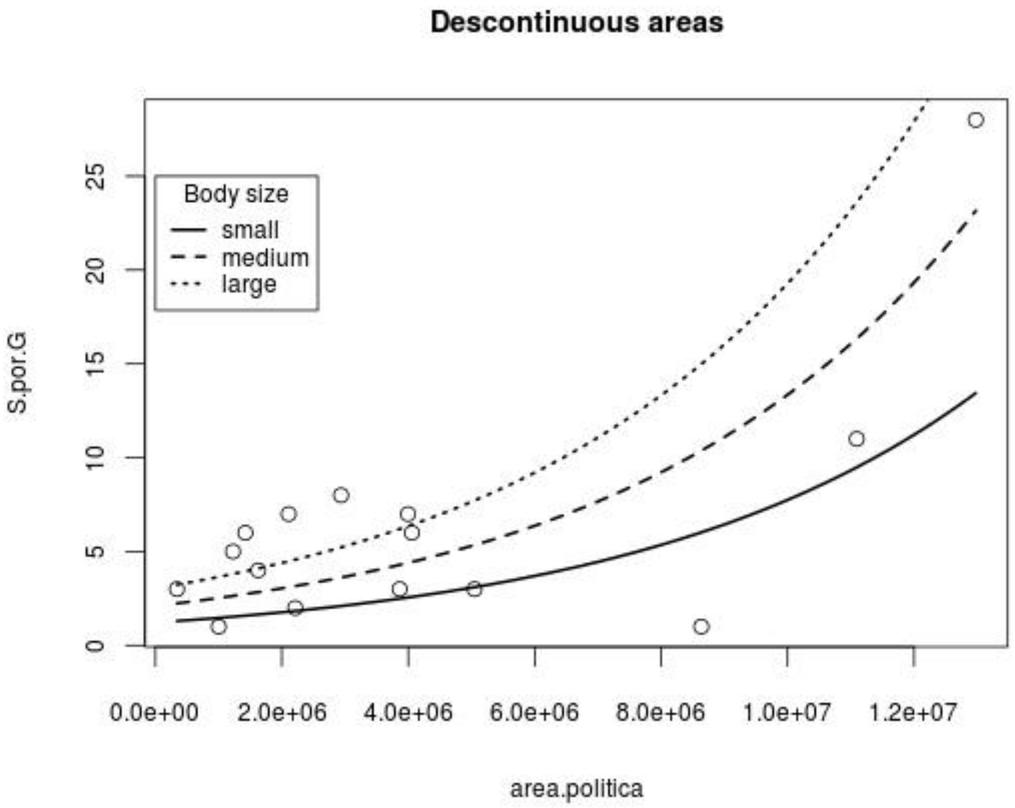

Figure 6: Species per genus increased with reported occurrence areas in descontinuous areas. $F_{1,13}$= 22.64; p = 0.00037

5. DISCUSSION

Among the four alternative estimates of geographic distribution, only political area had significant positive relationship with number of species per genus. Although incomplete, the OSF records reflect a significant estimator of genus geographic area. Discontinuous distribution records may either underestimate actual distribution area, or overestimate the genus scope. Genera with discontinuous records may amalgamate more than one actual clade.

None of the area estimates based on biome had a significant relationship with species per genus. This may be caused because the areas of originally continuous biomes underestimate effective barriers for species dispersion.

Presently forest biomes are majorly fragmented. Therefore, the altered matrix habitat could work as barrier to cricket dispersal. Another hypothesis would be that even in non-altered or pristine habitats, there are natural barriers for cricket dispersion, such as rivers. A large portion of the distribution areas of this study are in the Amazon forest, which remains still largely continuous, particularly in its central region.

The correlation of genus diversity with recorded distribution area is evidence for a third, simpler, explanation. Biome continuity may be insufficient for cricket dispersal. Most neotropical cricket species, especially forest ones, have lost their hindwings, preventing flight and probably leading to limited cricket dispersion.

The geographic and climate variations within the biome may be a barrier for most of species, limiting the geographic range these species occupy. Although there are much more undiscovered and unclassified species, making the current number of species per genus underestimated. As far as our data were restricted to one geographical area (South America), we consider that sampling effort was comparatively homogeneous, reducing the eventual effect of researcher effort differences among genera. Therefore, biological processes are a more suitable explanation for the detected area effects.

The increase of diversity with body size was opposite to our expectations. We were expecting the number of individuals per genus, inversely proportional to body size, increases with the speciation rates. The analyses showed that the bigger the cricket, the higher the number of species. Probably it is related to taxonomic efforts: bigger crickets are easier to catch and easier to identify and/or classify, while cricket species with smaller body size would be under-represented.

6. CONCLUSIONS

We conclude that the avaiable cricket distribution data, although sparse and not-systematic, are relevant to explain species diversity among genera. The biological processes involved in the empirical relationships that we highlighted deserve further investigation.

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