CHAIM JOSÉ LASMAR

COMUNIDADE DE FORMIGAS AO LONGO DE UM GRADIENTE ALTITUDINAL: INFLUÊNCIA DO TIPO DE VEGETAÇÃO E DE FATORES AMBIENTAIS E CLIMÁTICOS

LAVRAS – MG
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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para a obtenção do título de Mestre.

Orientadora

Dr$^{a.}$ Carla Rodrigues Ribas

LAVRAS – MG

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À minha família e ao Boni

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“All good work is done the way ants do things, little by little.”

Patrick Hearn

RESUMO GERAL

Gradientes altitudinais são ideais para testar teorias ecológicas, bem como os padrões de distribuição de espécies e também o efeito de mudanças climáticas no alcance das espécies. Dessa forma, este estudo avaliou o efeito do tipo de vegetação no padrão da riqueza de espécies de formigas em um gradiente altitudinal tropical. Nessa abordagem foram comparados dois tipos de amostragem ao longo do gradiente: uma padronizando o gradiente, amostrando somente em formações florestais e outro não padronizado amostrando em formações florestais e de campo. Além disso, foi estudado os padrões da diversidade alfa, beta e gama ao longo do gradiente e também a diversidade beta e seu principal mecanismo através das faixas altitudinais, sempre correlacionando os padrões encontrados com fatores ambientais e climáticos. Foi encontrado que o tipo de vegetação pode causar um viés nos padrões de riqueza de espécies de formigas encontrados no gradiente. Isso se deve provavelmente as diferentes condições ambientais que as formações florestais e de campo possuem. A diversidade alfa e gama seguem um declínio monotônico de espécies ao longo do gradiente. O principal mecanismo da diversidade beta entre as faixas altitudinais foi a substituição de espécies. A diversidade alfa e gama foram correlacionadas com a temperatura. Dessa forma, baixas temperaturas podem comprometer pode o forrageamento e desenvolvimento das lavras das formigas o que acarreta numa menor co-ocorrência de espécies em altitudes altas. A diversidade beta e seu principal mecanismo (substituição) entre as faixas altitudinais se correlacionou também com a temperatura. Tal fator climático provavelmente seleciona as formigas que conseguem suportar temperaturas baixas, agindo assim como um filtro das espécies. Dessa forma, uma mudança rápida do clima global talvez possa comprometer a fauna de formigas das montanhas tropicais.

Palavras-chave: Montanha Tropical. Riqueza de espécies. Diversidade Beta. Tipo de Fitofisionomia. Fatores Ecológicos.

ABSTRACT

Elevational gradients are ideal for testing ecological theories, species richness patterns and species ranges and its effects upon climatic changes. In this sense, this study evaluated the vegetation type effect on patterns of ant species richness in a tropical elevational gradient. We compared two kinds of approach in an elevational gradient: one sampling only in forest formations type across the gradient and another sampling in two vegetation types constituted by forest and grasslands formations. Besides that, we also evaluated alpha, beta and gamma diversity along elevation, and beta diversity and its main mechanism between elevational bands always correlating them to environmental and climatic factors. It has been found that vegetation type may bias ant species richness' patterns. Probably different conditions of those two vegetation types are influencing it. Alpha and gamma diversity followed a species monotonic decline along the gradient. In addition, the beta main mechanism between elevational bands was by the turnover of species. Alpha and gamma were correlated with temperature. Ants might be injured at highlands, wherein low levels of temperature may compromise its foraging and larval development. Therefore, lowlands with its higher levels of temperature might permit more co-occurrence of ant species than highlands. Beta diversity and its main mechanism (turnover) between elevational bands were correlated with temperature. Such climatic factor possibly selects ants that can survivor at low temperatures, acting as a species filter. In this sense, a rapidly change as consequence of global warming might compromise ant fauna of tropical mountains.

Keywords: Tropical Mountain. Species Richness. Beta Diversity. Ecological Factors. Elevational Gradient.

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PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

As montanhas cobrem aproximadamente 25% da superfície terrestre (BARTHLOTT; LAUER; PLACKEET, 1996), e seus topos apresentam um grande número de espécies endêmicas (BHARTI et al., 2013). No entanto, essas espécies podem estar ameaçadas pelo aumento da temperatura e modificações do clima, tal como o aquecimento global (PARMESAN, 2006).

Gradientes altitudinais são ideais para testar teorias ecológicas (COLWELL et al., 2008) e os estudos sobre riqueza de espécies nesses gradientes tem crescido nas últimas décadas complementando estudos sobre padrões em escalas latitudinais (RAHBEK, 2005). Além disso, os ambientes montanhosos são particularmente interessantes para estudos de biodiversidade pois possuem uma grande variação ambiental em uma pequena escala (KÖRNER, 2007) sendo que os padrões encontrados podem ser extrapolados a escalas maiores (SUNDQVIST; SANDERS; WARDLE, 2013). Em complemento, são áreas que oferecem uma visão sobre fatores históricos e contemporâneos que moldam a distribuição das espécies, devido a padrões ecológicos bem estabelecidos (RAHBEK, 2005; COLWELL; RANGEL, 2010).

Com o aumento da altitude, presenciamos diretamente uma diminuição da área, da pressão atmosférica e da temperatura, aumento da radiação total e radiação UV-B e indiretamente uma influência (sem padrões) sobre a precipitação (KÖRNER, 2007). Esta última variável é guiada mais por aspectos regionais do que o gradiente altitudinal em si (KÖRNER, 2007). A mudança do tipo de vegetação (em termos de formação florestal ou de campo) no entanto, não está diretamente ligada ao gradiente. A linha de árvores, caracterizada pela mudança da formação florestal para formação de campos (HARSCH; BADER, 2011), é resultado da seleção exercida pela interação de fatores ligados e não ligados ao gradiente (KÖRNER, 1998, 2007). Mesmo assim, alguns trabalhos que procuraram acessar os padrões altitudinais na riqueza de espécies foram desenvolvidos em dois ou mais tipos de vegetação (formações florestais e outros) (MUNYAI; FOORD, 2012; TELLO et al., 2015; CLASSEN et al., 2015; NAKAMURA et al.,2015). Dessa forma, não está claro o que realmente é reflexo do gradiente per si ou influência do tipo de formação da vegetação.

Estudos sobre a riqueza de espécies de diversos taxa em gradientes altitudinais na maioria das vezes apresentam um padrão de distribuição de variação unimodal (50%), declínio monotônico (25%), e outros mais complexos (25%) (RAHBEK, 2005). Esses padrões diferentes provavelmente ocorrem devido a desenhos amostrais distintos em relação ao espaço amostrado (RAHBEK, 2005).

Esses padrões de declínio monotônico e unimodal das espécies estão geralmente ligados a produtividade, temperatura, a interação da precipitação e temperatura, a área e o efeito do domínio mediano, (RAHBEK, 2005; NOGUÉS-BRAVO et al., 2008). Além disso, a curta distância dos gradientes altitudinais (em relação aos altitudinais) não é um limitante na dispersão das espécies devido a sua pequena escala espacial. O alcance dessa espécies então, será moldado a partir de variáveis climáticas. Consequentemente, a distribuição das espécies e seu alcance são bons indicativos para o estudo de padrões ecológicos já que apresentam os padrões semelhantes de riqueza de espécies de gradientes latitudinais (MACARTHUR, 1972; STEVENS, 1992). Adicionalmente, gradientes altitudinais servem como experimento ideal para diagnosticar as mudanças que acontecem com modificações no clima (WILSON et al., 2005; PARMESAN, 2006; COLWELL et al., 2008), já que as variáveis climáticas exercem uma forte influência sobre o alcance da espécies (PARMESAN, 2006).

Entender o que influencia o alcance da distribuição das espécies, assim como ocorre a substituição de espécies no gradiente altitudinal pode ajudar a entender a sensibilidade dos sistemas ecológicos as mudanças ambientais (FITZPATRICK et al., 2013). Nesse sentido, a partição da diversidade β (BASELGA, 2010) tem a vantagem de desmembrar qual mecanismo está por detrás das mudanças das espécies ao longo de um gradiente (substituição e/ou aninhamento). A substituição de espécies está ligada a troca de espécies de um lugar para o outro e é comumente ligada a fatores que promovem o endemismo das espécies em consequência a restrições históricas ou características do habitat (QIAN; RICKLEFS; WHITE, 2005; BASELGA, 2010). Por outro lado, a mudança resultante do aninhamento se refere ao ganho ou perda de espécies entre um lugar e outro, devido a processos de extinção e colonização, geralmente ligados a fatores ambientais que resulta numa desagregação das comunidades (GASTON; BLACKBURN, 2000; BASELGA, 2010). Porém, a diversidade β e seus principais mecanismos foram pouco explorados (BISHOP et al., 2015) assim como foi pouco explorado a influência de fatores climáticos e ambientais sobre os mecanismos da diversidade β em gradientes altitudinais. Dessa forma, entender qual o principal mecanismo da diversidade β atua em gradientes altitudinais pode ajudar a entender os padrões de distribuição das espécies (BISHOP et al., 2015), assim como entender qual o fator ecológico influencia esses mecanismos pode ajudar a entender o que influencia a distribuição das espécies. Além do mais, montanhas tropicais podem ter uma resposta particular às mudanças climáticas em relação às montanhas da zona temperada, já que em montanhas tropicais o alcance das espécies é bem delimitado e há espécies endêmicas no topo que não podem mudar seu alcance para altitudes mais altas em respostas a mudança climáticas e que podem leva-las a extinção (COLWELL et al., 2008).

Desta forma, essa dissertação contém dois capítulos em forma de manuscritos. O primeiro trata do efeito do tipo de vegetação (em termos de formação florestal e de campo) nos padrões de riqueza de espécies em um gradiente altitudinal tropical. Já o segundo, tem como objetivo acessar os padrões de diversidade alfa, beta e gama ao longo de um gradiente altitudinal e também os padrões da diversidade β e seu principal mecanismo gerador entre as faixas altitudinais. Além disso, neste mesmo manuscrito investigamos quais os fatores ambientais e climáticos estão ligados aos padrões acima acessados.

Para fazer isso, usamos formigas como ferramenta de estudo, pois são organismos abundantes nas áreas tropicais (WILSON; HOLLDOBLER, 2005) e são extremamente sensíveis a mudanças ambientais (PHILPOTTet al., 2010). Vários trabalhos já foram feitos em relação a gradientes altitudinais usando formigas (e.g. FISHER, 1996; SANDERS, 2002; SANDERS; MOSS; WAGNER, 2003; LONGINO; COLWELL, 2011; BHARTI et al., 2013; BISHOP et al., 2014). Esses organismos são fortemente influenciados pela temperatura (SANDERS et al., 2007; BISHOP et al., 2014) e também por características do habitat como heterogeneidade e disponibilidade de recursos (RIBAS et al., 2003, COSTA et al., 2011; BHARTI et al., 2013; QUEIROZ; RIBAS; FRANÇA, 2013).

REFERÊNCIAS

BASELGA, A. Partitioning the turnover and nestedness components of beta diversity. **Global Ecology and Biogeography**, Malden, v. 19, p. 134–143, out. 2010.

BARTHLOTT, W.; LAUER W.; PLACKEET A. Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. **Erdkunde**, Bonn, v.50, p. 317–327. 1996.

BHARTI, H. et al. Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas. **Asian myrmecology**, Ulaanbaatar, v 5, p. 79–101, 2013.

BISHOP T. R. et al. Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. **Journal of Biogeography**, Malden,v. 41, n. 12, p. 2256–2268, jun. 2014.

BISHOP, T. R. et al. Contrasting species and functional beta diversity in montane ant assemblages. **Journal of Biogeography**, Malden,v. 42, n. 9, p. 1776–1786, set**.** 2015

COLWELL, R. K. et al. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. **Science**, Washington, v. 322, n.5899, p. 258–261, out. 2008.

COLWELL, R.; RANGEL, T. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. **Philosophical Transactions of the Royal Society B: Biological Sciences**, London,v.365, p. 3695–3707, nov. 2010.

COSTA F. V. et al. Relationship between plant development, tannin concentration and insects associated with *Copaiferalangsdorffii*(Fabaceae). **Arthropod Plant Interactions**, Helsinki, v. 5, n. 1, p. 9–18, mar. 2011.

CLASSEN A. et. al. Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania?**Global Ecology and Biogeography**,Malden, v. 24, p. 642–652, jun. 2015.

FISHER, B. L. Ant diversity patterns along an elevational gradient in the Reserve NaturelleIntegraled'Andringitra, Madagascar**. Fieldiana Zoology**, Chicago,(n.s.) 85, p. 93–108. 1996.

FISHER, B. L. Ant diversity patterns along an elevational gradient in the RéserveSpéciale de Manongarivo, Madagascar. **Boissiera**, Geneva, v.59, p. 311–328. 2002.

FITZPATRICK M. C. et al. Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. **Proceedings of The Royal Society B**, London, v. 280 n. 1768, out. 2013.

GASTON, K. J.; BLACKBURN, T. M. Pattern and process in macroecology. **Blackwell Science**, Oxford, Oxford University, 2000.

HARSCH, M. A.; BARDER, M. Y. Treeline form – a potential key to understanding treeline dynamics.**Global Ecology and Biogeography**,Malden,v.20, p. 582–596, jun. 2011.

KÖRNER, C. A re-assessment of high elevation treeline positions and their explanation. **Oecologia**, Berlin, v. 115, n. 4, p. 445-459, jul. 1998.

KÖRNER, C. The use of 'altitude' in ecological research. **Trends in Ecology and Evolution**, Amsterdam, v. 22, n. 11, p. 569–574. nov. 2007.

LONGINO J. T.; COLWELL R. K. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. **Ecosphere**, Washington, v. 2, n. 3, p.1–20, mar. 2011.

MACARTHUR, R. H**.** Geographical Ecology: patterns in the distribution of species. **Harper and Rowe Publishers**, New York. 1972.

MUNYAI T. C.; FOORD, S. H. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. **Journal of Insect Conservation**, London, v. 16, n. 5, p. 677–695, out. 2012.

NAKAMURA, A. Identifying indicator species of elevation: Comparing the utility of woody plants, ants and moths for long-term monitoring. **Austral Ecology**, Carlton, doi:10.1111/aec.12291, 2015.

NOGUES-BRAVO, D. et al. Scale effects and human impact on the elevational species richness gradient. **Nature**, Washington, v.453, p. 216–219, mai. 2008.

PARMESAN, C. Ecological and evolutionary responses to recent climate change. **Annual Review of Ecology, Evolution, and Systematics**, Palo Alto, v. 37, p. 637–669, ago. 2006.

PHILPOTT, S. M. et al Ant diversity and fuction in disturbed and changing habitats. In: LACH, L.; PARR, C. L.; ABBOTT, K. L. (Ed.). **Ant ecology**. Oxford: Oxford University, 2010. p. 137-156.

QIAN, H.; RICKLEFS, R. E.; WHITE, P. S. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. **Ecology Letters**, Oxford, v. 8, n. 1, p. 15–22, jan. 2005.

QUEIROZ A. C. M.; RIBAS C. R.; FRANÇA F. M. Microhabitat Characteristics that Regulate Ant Richness Patterns: The Importance of Leaf Litter for Epigaeic Ants. **Sociobiology**, California, v.60, n. 4, p. 367-373, agu. 2013.

RAHBEK, C. The role of spatial scale and the perception of large-scale species-richness patterns. **Ecology Letters**, Oxford, v. 8, n. 2, p. 224–239, fev. 2005.

RIBAS C. R. et al. Tree heterogeneity, resource availability, and larger scale process regulating arboreal ant species richness. **Austral Ecology**, Carlton, v. 28, n. 3, p. 305–314, jun. 2003.

STEVENS, G. C. The elevational gradient in altitudinal range: an extension of Rapoport’s latitudinal rule to altitude. **American Naturalist**, Chicago, v. 140, n. 6, p. 893–911, dez. 1992.

SANDERS, N. J. Elevational gradients in ant species richness: area, geometry, and Rapoport’s rule. **Ecography**, Malden, v.25, n. 1, p. 25–32, fev. 2002.

SANDERS, N. J.; MOSS, J.; WAGNER, D. Patterns of ant species richness along elevational gradients in an arid ecosystem. **Global Ecology and Biogeography**, Malden, v. 12, n. 2, p. 93–102, mar. 2003.

SANDERS, N. J. et al. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains**. Global Ecology and Biogeography**,Malden, v. 16, n. 5, p. 640–649, set. 2007.

STEVENS, G. C. The elevational gradient in altitudinal range: an extension of Rapoport’s latitudinal rule to altitude. **American Naturalist**, Chicago, v.140, n. 6, p. 893–911, dez. 1992.

SUNDQVIST, M. K.; SANDERS, N. J.; WARDLE, D. A. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. **Annual Review of Ecology, Evolution, and Systematics**, Palo Alto, v. 44, p. 261–280, nov. 2013.

TELLO J. S. et al. Elevational Gradients in β-Diversity Reflect Variation in the Strength of Local Community Assembly Mechanisms across Spatial Scales. **Plos One**, San Francisco, V. 10, n. 3, DOI:10.1371/journal.pone.0121458, 2015.

WILSON, R. J. et al. Changes to the elevational limits and extent of species ranges associated with climate change**. Ecology Letters**, Oxford, v. 8, n. 11, p. 1138–1146, nov. 2005.

WILSON, E. O.; HOLLDOBLER. B. The rise of the ants: A phylogenetic and ecological explanation. **Proceedings of the National Academy of Sciences of the United States of America**, Washington, v.102, n. 21, p. 7411–7414, mar. 2005.

SEGUNDA PARTE - ARTIGOS

ARTIGO 1

DISENTANGLING ELEVATIONAL AND VEGETATIONAL EFFECTS ON ANT DIVERSITY PATTERNS

Preparado de acordo com as normas da revista PLoS One

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ABSTRACT

Elevational gradient studies have been appreciated by ecologists and biogeographers for a long time. A variety of studies has been developed on different vegetation types assessing patterns of species diversity on elevation, (i.e. when elevations increases there are changes from closed forest to grassland formations). It is still not clear which effectsare caused by factors that covary with elevation alone and which are caused by different vegetation types changes. The aim of this study was to disentangle elevation from vegetation types change effects on diversity patterns. We analyzed the found ant diversity patterns in an elevational gradient resulting from two kind of approaches: (1) a standardized sampling including only one vegetation type, based in forest formation across the elevational gradient and (2) a non-standardized sampling, including two vegetation types (forest and grasslands formation) across the elevational gradient. We also compared the ant species composition under and above a tropical treeline mountain. To do so, we sampled ants at eight elevational bands of Atlantic Rain forest, from what, in our sixth elevations we sampled both forest and grasslands habitats. We found distinct mean species richness regarding the two approaches, but the same pattern of overall species richness. However, by not standardizing the vegetation type in study design caused a smaller proportion of explanation of the regression analysis and decreased the elevational effect size on species richness.We also found differences on species composition between above and below treeline. Different patterns found at the two approaches might be due the difference of environmental conditions from both kinds of habitats. In conclusion, our results highlight a bias of non-standardizing the vegetation type across elevational gradient protocols when assessing the elevational patterns of species diversity.

Keywords: Altitudinal gradients. Tropical Mountain. Effect size.

INTRODUCTION

Two centuries passed since one of the first studies on elevational gradients (von Humboldt, 1849); and yet, such kind of approach is still being appreciated by ecologists and biogeagraphers all around the world. This kind of gradient has been used to assess species richness patterns (Rahbek, 2005; Nógues - Bravo, 2008), species distributions ranges (Stevens, 1992; Sanders, 2002) interspecific competition (Cadena, 2007), community phylogenetic structure (Mach et al., 2011) and climate change (Colwell et al.; 2008). In this respect, elevational gradients are interesting because they present a great variability of environmental factors at a small spatial scale (Körner, 2007). It presents well estabilished ecological patterns due both to historical and ccurrent factors, that shape the species distribution (Rahbek, 2005; Colwell & Rangel., 2010) and it mirrors ecological patterns of latitudinal gradients (Rahbek, 2005).

There are factors intrinsically linked to the elevational gradient such as temperature, area availability, atmospheric pressure and UV-B radiation (Körner, 2007). These factors change with the elevation and can influence plants' physiology, metabolic processes, body size, and distribution as a result of species being selected by them (Körner, 1998; 2007). In this sense, such adaptations are notorious, specially when we account the dramatic change on vegetation type at the treeline. The treeline is characterized by Harsch& Bader (2011) as "an ecotone delimited at the upper end by the tree species limit, the uppermost elevation or latitude at which tree species occur as trees or krummholz regardless of height, and at the lower end by continuous forest > 3 m tall”. Hence, we can observe a pronounced change on vegetation type (i.e. shifting from forest habitat to grassland habitats formations in tropical mountains). Besides there been high levels of turnover of plant species throughout the gradient (Sundqqvist et al., 2013) and that there are zonations of multilayered tropical montane forests according the elevational gradient (Hemp, 2006), the changes on vegetation type, in terms of forest and grasslands formation, are not directly linked to elevational gradients, the most likely factors are the ones mentioned above (eg. temperature, atmospheric pressure, etc.).

Nevertheless, many studies were performed across different vegetation types, that did not only include forest formations to assess elevation gradient patterns (Munyai & Foord, 2012; Tello et al., 2015; Classen et al., 2015; Nakamura et al., 2015). In this sense, there is a natural suspect that the results of those studies, which were conducted on different vegetation types, are reflecting only elevation patterns, or elevation patterns with a bias caused by the change of vegetation type. If not standardizing the vegetation types, changing the sampling from forest to grassland or other formations along the gradient may drastically influence the patterns found in an elevational gradient study. In addition, it has never been tested if not standardizing the vegetation type across elevational gradient may be biasing the patterns of species diversity.

Here, we disentangle the effects of elevation from vegetation type changes on ant diversity patterns. We tested whether sampling in different vegetation types in an elevational gradient may produce different patterns on mean species richness and overall species richness. In addition, we assessed whether species composition above the treeline of grasslands and forest remnants were different from treeline level species. We hypothesized that vegetation type has influence when we are assessing elevational gradients by blinding some patterns that could occur only due to elevation. To do so, we used ants as a proxy because such taxa is well distributed in tropical areas (Moreau & Bell, 2013), are sensible to changes on the environment (Philpott et al., 2010), on vegetation types (Majer, 1983; Arnan et al., 2006) and habitat features (Ribas et al., 2003; Mezger & Pfeiffer, 2011; Queiroz et al., 2013; Gollan et al., 2015), and have been used successfully for assessing elevational gradients patterns (Fisher, 1998; Colwell et al., 2008; Malsch et al., 2008; Bishop et al., 2015).

MATERIAL & METHODS

Study area

The study was conducted at Itatiaia National Park (INP), in the southeast of Brazil (22º16’ - 22º28’ S and 44º34’ - 44º42’ W). INP was established in 1937 and it is the oldest national park in Brazil inserted in Atlantic Rain Forest biome. The park is located in Itatiaia Massif, on the highest portion of the Mantiqueira Mountain. The protected area starts at 600 m a.s.l elevation and it peaks at 2.878 m a.s.l. Treeline of Mantiqueira Mountain is situated around 2000 m a.s.l.. There are many vegetation types at Mantiqueira Mountain, ranging from “lower montane” forest (at 0-500 m a.s.l.), to montane forest (500 – 1500 m a.s.l.), upper montane forest (1500 – 2000 m a.s.l.), and *campos de altitude* (2000 – 2500 m a.s.l.) (Safford, 1999). All vegetation types are constituted by forest formations but only *campos de altitude* is constituted by grasslands. When we refer to vegetation types in this study, we mean the habitat formation that can be closed forest or open grassland. In this sense, until the treeline, there is a continuous dense Atlantic rain forest and above treeline the vegetation type changes to open grasslands. There are still some remnants of closed forest inside open grasslands. The continuous closed Atlantic rain forest presents diverse plant families such as Arecaceae, Rubiaceae, Lauraceae, Burseraceae, Rutaceae, Fabaceae, Erythroxylaceae, Myrtaceae, Salicaceae, Euphorbiaceae, Araucariaceae, Bigoniaceae, and Piperaceae. The *campos de altitude* (grassland) presents exposed rocks and is dominated by plants from Poaceae, also showing some elements of herbaceous plants families as Asteraceae, Apiaceae, Alstroemeriaceae. It also presents bogs that presents plant families such as Cyperaceae, Lentibulariaceae, Xyridaceae and bryophytes. Above the treeline, forest remnants are composed by plants families such as Myrtaceae, Melastomataceae, Asteraceae, Fabaceae, Proteaceae, Aquifoliaceae, and Solanaceae, Proteaceae.

Ant sampling

We chose eight elevational bands 600, 848, 1134, 1515, 1810, 2000, 2200 and 2457 m a.s.l.. In each elevation, we installed one 200 m transect spatially separated by at least 1.4 km and constituted by 10 sampling points spaced 20 m between them. In each sampling point we had four epigaeic pitfall traps in a square grid of 1.5 m x 1.5 m. Pitfalls were 8 cm in diameter and 12 cm in depth, filled with a 200 ml solution of water, salt (0.4%) and liquid soap (0.6%) (Canedo-Júnior et al., 2016). They remained operating for 48 hrs in the field.

Until our fifth elevation (1810 m) we had only one transect in closed Atlantic rain forest per elevation, from 2000 m, our sixth elevation situated at the treeline, we had two transects per elevation for sampling both closed forest copses and open grasslands. Although our sixth forest transect is situated at the treeline, we called every grassland and forest transects as above treeline from our sixth elevation. The different transects of two vegetation types considering the closed forest and open grasslands formations (Fig. 1) were installed spatially separated by at least 160 m considering that we have to maintain them at the same elevation.

Figure 1. Images of our replicated transects. Side by side, different vegetation types at the same elevation above treeline. At the right, we have forest remnants and at the left, we have grasslands. From top to down we have transects that are at 2000, 2200 and 2470 m a.s.l.

Data analysis

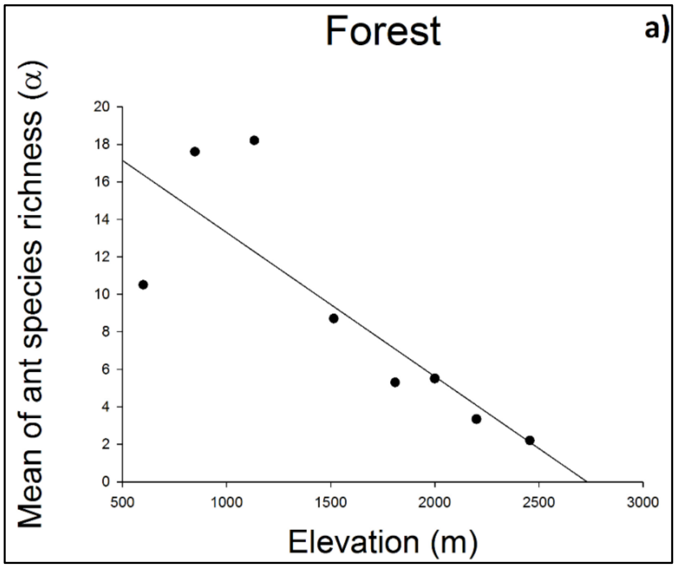
To test whether sampling in different vegetation types in terms of habitat formation in elevational gradient may produces a bias on the distributional patterns, we performed generalized linear models (GLMs) with two diversity components (α and ɣ) extracted from two approaches. In one approach we had only closed forest vegetation type transects and at the other we had five lowlands closed forest transects plus the three highlands open grasslands transects, simulating a sampling for assessing the elevational gradient performed in different vegetation types in terms of habitat formation. For both approaches we used as response variables the mean species richness (mean of collected species richness in the sampling points per transect, α) and overall species richness (overall collected species per transect, ɣ). The explanatory variable was the transects' elevations. All GLMs were assessed under residual analyses to obtain the adequacy of error distribution (Crawley, 2002). In the case of both approaches (using only forest transects or forest and grasslands transects), producing the same pattern, we performed a resampling application from 1000 bootstrap samples replacing it in '*boot.ci()*' function from *'boot'* package (Canty& Ripley, 2012). With this function, we can assess 95% confidence intervals of intervals of regression R^2 and slope and the median precision of the GLMs of two approaches. Therefore, we were able to check if there was difference in model precision and the effect size of those regressions. We performed all analysis above at software R 3.01 (R development Core Team 2013).

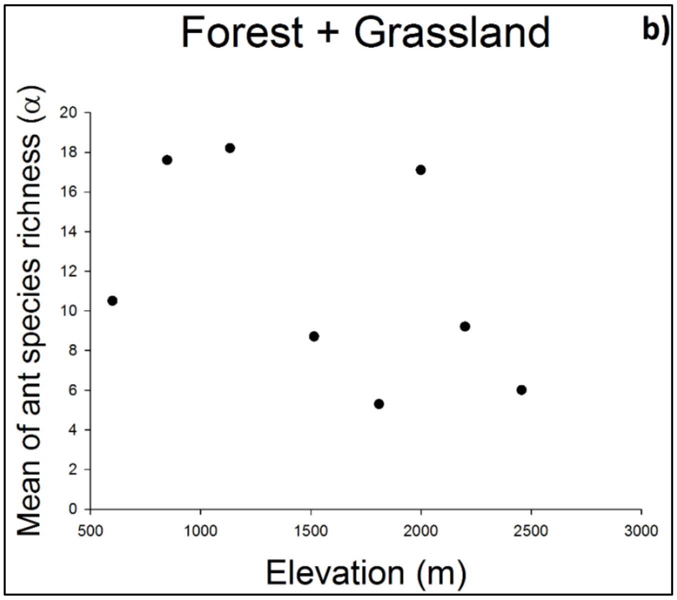
Finally, to assess the difference of ant species composition, we performed a non-multidimensional similarity (NMDS) analysis and a similarity analysis (ANOSIM) taking into account the presence and absence of species within three factors; under treeline, above treeline forest, above treeline grassland. We used the Jaccard index, which is appropriated to presence/absence. We performed the analysis with PRIMER 6.

RESULTS

At total, we collected 191 antsmorphospecies, being 146 ants species from under the treeline transects, 33 from above the treeline forest transects and 55 ant species from above the treeline grasslands transects.

The two approaches differed in their patterns,regarding mean species richness (α) (Fig. 2a and b) being only forest transects negatively related to elevation (F = 13.03; *p* = 0.0110) and forest plus grassland transects not relatedto elevation (F = 1.72; *p* = 0.2375). Regarding the overall species richness (ɣ) both approaches exhibited the same pattern (Fig. 2c and d), being both only forest transects (F = 59.77; *p* = 0.0002) and forest plus grasslands transects (F = 17.80; *p* = 0.0055) following a monotonic decline in relation to elevation.


Forest
a)
Mean of ant species richness (α)
20
18
16
14
12
10
8
6
4
2
0
500
1000
1500
2000
2500
3000
Elevation (m)


Forest + Grassland
b)
Mean of ant species richness (α)
20
18
16
14
12
10
8
6
4
2
0
500
1000
1500
2000
2500
3000
Elevation (m)

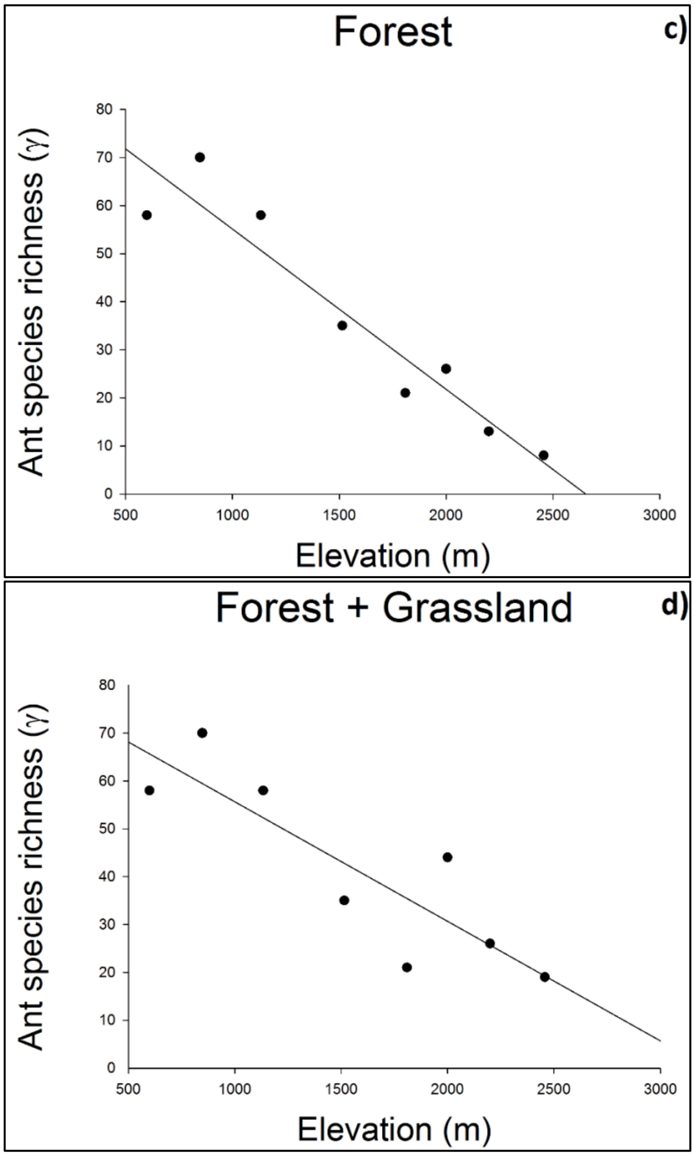


Figure 2. Relationship between ant diversity components and elevation. **a)** Mean ant species richness per sampling point (α) of only forest transects (F = 13.03; *p* = 0.0110; n = 8). **b)** Mean of ant species richness per sampling point (α) of forest plus grasslands transects (F = 1.72; *p* = 0.2375; n = 8). **c)** Overall ant species richness (ɣ) of only forest transects (F = 59.77; *p* = 0.0002; n = 8). **d)** Overall ant species richness (ɣ) of forest plus grasslands transects (F = 17.80; *p* = 0.0055; n = 8).

Despite obtaining the same pattern for two approaches upon ɣ diversity, we can observe a greater statistical power on only forest transects regression than in forest plus grasslands transects regression (Fig. 3a). Using only forest transects also demonstrated a higher effect size based on the regression slope values (Fig 3b).

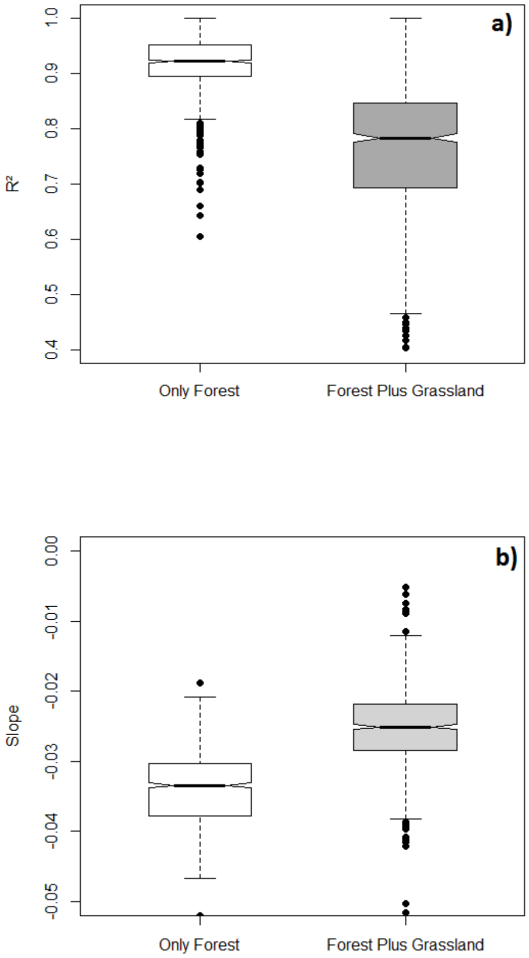


Figure 3. Comparisons of two regression attributes between only forests transects and forest plus grassland transects of generalized linear models of overall ant species richness per transect (ɣ) with elevation. **a)** Proportion of explanation (R^2) and **b)** Effect size (slope of the regression line). Vertical dashed lines are bootstrapped confidence intervals based on 1000 bootstrap samples with replacement. Notch area on boxplots marks the 95% confidence intervals of medians values that is the black horizontal lines. Black dots are the outliers and were cut at figure b) for best visualization of medians confidence intervals.

The NMDS showed a distinct composition of pattern for all treatments or group of transects (Global R = 0.67; *p* = 0.010; Fig. 4). However, comparing the factors pairwise, both above treeline forest and grassland transects differed from under treeline transects, but they are similar between them (Table 1).

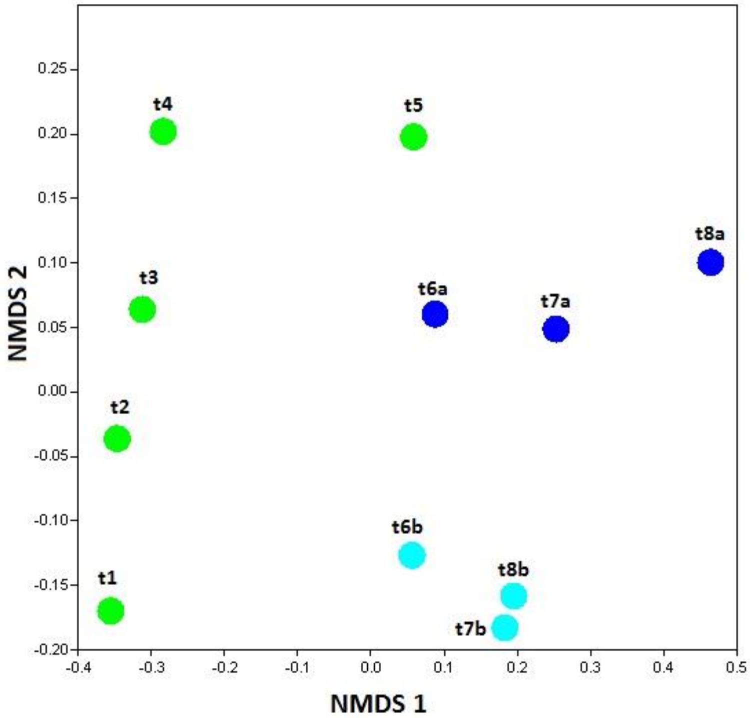


Figure 4. Non-metric multidimensional scaling (NMDS) performed on ant species composition collected at Itatiaia National Park elevation gradient. Species composition of under treeline forest transects at 600 (t1), 848 (t2) 1134 (t3), 1515 (t4), 1810 (t5) m a.s.l., above treeline forest remnants transects at 2000 (t6a) 2200 (t7a) and 2457 (t8a) m a.s.l and above treeline grasslands transects at 2000 (t6a) 2200 (t7a) and 2457 (t8a) m a.s.l.

Table 1. ANOSIM results of ant species composition between above treeline closed forest transects, grassland transects and under reline closed forest transects.

Groups	**R value**	**P value**
Under treeline *versus*above treeline (forest)	0.682	0.018
Under treeline *versus* above treeline (grassland)	0.764	0.018
Above treeline (forest) *versus* above treeline (grassland)	0.778	0.1

DISCUSSION

Assessing elevational gradient patterns in different vegetation types, in terms of sampling closed forest or grasslands formations across the gradient, can produce some bias at the founded patterns. The patterns found for mean species richness (α) clearly differed from sampling in only one vegetation type than sampling in two vegetation types. In addition, regarding overall species richness (ɣ), the same pattern (i.e. monotonic decline) was observed at the two approaches. However, sampling in the same vegetation allows us to obtain a higher proportion of explanation in our statistical analysis and evaluate with accuracy the effect of elevational gradient on species richness as well. Ant species composition of above the treeline differed from under treeline independently of the vegetation type.

The mean species richness (α) above the treeline in grasslands transects surprisingly reached almost the same mean of species richness of the most specious lowers forest transects. At another similar habitat, rocky grasslands, was also found a large number of ant species (Costa et al., 2015). Consequently, we could not find any pattern when analyzing the two vegetation types in the elevational gradient. In accordance with our results, Botes et al. (2006) also found an influence of different vegetation types on ant species. We supose that different results caused by sampling in the same or in different vegetation types are due to intrinsically conditions imposed by two vegetation types (grassland and forest). The trees in a forest are coupled to atmospheric circulation, thus such habitat is closely related to ambient temperature, but low stature vegetation presents warmer conditions due its capacity to create an aerodynamic resistance, leading such habitat to a hard exchange of heat received from solar radiation (Körner, 2007). Moreover, the air retain less water at highlands (Körner, 2007) and so the soil presents saturated levels of water (Bruhl et al., 1999), therefore, probably higher forest transects presents high levels of moisture than grasslands. In mountains, temperature and high levels of moisture influence ant species richness because they act on ants’ foraging activity (Fisher, 1998; Bruhl et al., 1999; Malsch et al., 2008; Sanders et al., 2007). In this sense, the warmer conditions and low levels of moisture of grasslands related to highlands forest transects might permit more species co-occurring because grasslands conditions are better to support ant colonies than forest at higher altitudes.

We observed the same monotonic decline ofγ diversity at the two approaches. We hypothesize that elevational gradient produces a strong pattern on species diversity, resulted from the strong influence of temperature, as has been reported such influence on insect assemblages and also its correlation to elevation (Sanders et al., 2007; Malsch et al., 2008). Thus, even changes on vegetation type could not change the pattern. Above the treeline all grassland transects had more species than their respective forest transects. The influence of available area on elevational patterns of ant species richness was also documented (Sanders, 2002). Above 2000 m a.s.l. at PNI, most part of the Mantiqueira mountain chain is composed by grasslands rather than forest remnants. In this sense, we believe that a greater number of species from grasslands transects (in relation to above treeline forest transects) is due to area effect at highlands. Even so, it is still intriguing the different responses of α and ɣ on the two approaches. We think that temperature is an important factor acting at the two scales (α and ɣ) in our elevational gradient. However, the grasslands maybe present more homogenous habitats in comparison to highland forests. Such homogenization might occur with ambient conditions (related to temperature and degrees of moisture). In this sense, grasslands ants might colonize almost all sites in the transect, what they could not do in more heterogeneous forest transects. In other words, maybe the beta diversity in highlands forest transects is the major contributor to ɣ diversity and in other hand, α diversity of grasslands contributes more to its ɣ. Yet beta diversity of forest transects is not too higher as the α diversity of grasslands and so above treeline forest transects presents low values of ɣ diversity in comparison to grasslands

According to our results, we lost accuracy on the proportion of explanation and on the elevational effect size when sampling in different vegetation types. In fact, species diversity are not influenced by elevation per si but by factors that covary with it. Maybe these results are due to the problem of not isolating the influence of factors linked to elevation, resulting on different factors actions (actions by factors linked to elevation and factors linked to different habitats intrinsic structure and conditions). Gotteli& Ellison (2004) have pointed out that when there are many factors confounded between them at a study design, their effects are hard to be clarified. Probably the higher proportion of explanation found when we used only forest transects is due the similarity of other environmental factors, except those linked to elevation. Consequently the effect size of elevation on species richness of forest plus grasslands transects is lower because besides elevation, there are other environmental variations, in this case, that permit more species to survive at such elevations in grasslands in relation to the forest transects at same elevation (see above detailed explanation).

Species composition of our two approaches above treeline differed from lower forest transects, but they are similar among them. We believe that from the treeline, there is a strong environmental filter acting on ant species that come from lowlands of the mountain, because ant community at highlands is structured by an environmental filter due to low temperature levels (Machac et al., 2007). In another study, Fisher (1996) has argued that ant diversity is divided in two different communities: lowlands and highlands, in a mountain in Madagascar. Our results support the importance of conservation of highlands fauna on tropical mountains according other studies that highlight climate change threatens to insect fauna, since ant species between lowlands and highlands presented different composition (i.e. Hill et al., 2002; Botes et al, 2006)

This study is the first to demonstrated how relevant it is to assess elevational gradient patterns in the same vegetation type. Körner (2007) have previously highlighted the importance of not mistaking geophysical factors that are linked with factors not linked to elevation, which may lead to assessments of other environmental factor gradients (i.e. the positive relationship of elevation and species richness in arid mountain as a result from a positive relationship of precipitation and elevation at such regions) but not elevation per se. In our study, we pointed out the influence of different vegetation types that might trammels elevational patterns on ant species. Such bias also reduced the proportion of explanation of our analysis and weakened the effect size of losses of species across elevational gradient. Based on that, we suggest sampling in the same vegetation type, in terms of closed forest or grasslands formation, when assessing elevational gradient patterns. However if it is not possible to assess only one vegetation type, depending whether or not the extent of the gradient is enough (see Rahbek, 2005) we suggest to only verify the regional species pool of elevational bands, but probably it will be biased anyway.

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REFERENCES

Arnan X, Rodrigo A, Retana J. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. J Biogeogr. 2006;33: 1246–1258.

Bishop TR, Robertson MP, van Rensburg BJ, Parr CL. Contrasting species and functional beta diversity in montane ant assemblages. J Biogeogr. 2015. doi:10.1111/jbi.12537

Botes A, McGeoch MA, Robertson HG, van Niekerk A, Davids HP, Chown SL. Ants, altitude and change in the northern Cape Floristic Region. J Biogeogr. 2006;33: 71–90.

Bruhl A, Mohamed M, Linsemair KE. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. J Trop Ecol.1999;15:265-277.

Cadena CD. Testing the role of interspecific competition in the evolutionary origin of elevational zonation: an example with Buarremon brush-finches (Aves, Emberizidae) in the neotropical mountains. Evolution [R].2007;61: 1120–1136.

Canedo-Júnior EO, Cuissi RC, Curi NHA, Demetrio GR, Lasmar CJ, Malves K, Ribas CR. Can anthropic fires affect epigaeic and hypogaeicCerrado ant (Hymenoptera: Formicidae) communities in the same way? Rev Biol Trop.2016;64: 95-104.

Canty A, Ripley B. boot: bootstrap R (S-plus) functions. R package version1.3-4. 2012. Available: wwwr-project.org.

Classen A, Peters MK, Kindeketa WJ, Appelhans T, Eardley CD, Gikungu MW, Hemp A, Nauss T, Steffan-Dewenter I. Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Glob EcolBiogeogr.2015;24: 642–652.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. Science [R].2008.doi: 10.1126/science.1162547

Colwell RK, Rangel TF. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. Philos Trans R Soc B.2010;365: 3695–3707.

Costa FV, Mello R, Lana TC, Neves FS. Ant fauna in megadiverse mountains: a checklist for the rocky grasslands. Sociobiology.2015;62: 228-245.

Crawley MJ. Statistical computing: An Introduction to Data Analysis Using S-Plus. London: John Wiley & Sons, Ltd; 2002.

Fisher BL. Ant diversity patterns along an elevational gradient in the Reserve NaturelleIntegraled’Andringitra, Madagascar. Fieldiana Life Earth Sci.1996;85:93–108.

Fisher, B. L. Ant diversity patterns along an elevational gradient in the RéserveSpécialed’Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. Fieldiana Life Earth Sci.1998;90:39–67.

Gollan JR, Ramp D, Ashcroft MB. Contrasting topoclimate, long-term macroclimatic averages, and habitat variables for modelling ant biodiversity at landscape scales. Insect Conserv Divers. 2015;8: 43–53.

Gotelli, NJ, Ellison AM. A primer of ecological statistics. Sinauer Associates, Inc.2004. Chapter 6, pp 155-179.

Harsch MA, Bader MY. Treeline form – a potential key to understanding treeline dynamics. Glob EcolBiogeogr. 2011;20: 582–596.

Hemp A. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. Plant Ecol. 2006;184: 27–42.

Hill JK, Thomas CD, Fox R., Telfer MG, Willis SG, Asher J, Huntley B. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proceedings of the Royal Society of London B. 2002;269: 2163–2171.

Körner C. A re-assessment of high elevation treeline positions and their explanation. Oecologia. 1998;115: 445-459.

Körner C. The use of ‘altitude’ in ecological research. Trends EcolEvol.2007;22: 569–574.

Machac A, Janda M, Dunn RR, Sanders NJ. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography [R].2011;34: 364-371.

Majer JD. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environ Manage.1983;7: 375-383.

Malsch AKF. Fiala B, Maschwitz U, Mohamed M, Nais J, Linsenmair KE. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. Asian Myrmecol. 2008;2: 33–49.

Mezger, D, Pfeiffer M. Partitioning the impact of abiotic factors and spatial patterns on species richness and community structure of ground ant assemblages in fourBornean Rainforests. Ecography [R]. 2011;34: 39-48.

Moreau CS, Bell CD. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution [R].2013.doi:10.1111/evo.12105

Munyai TC. Foord SH. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. J Insect Conserv. 2012;16: 677–695.

Nakamura A, Burwell CJ, Ashton LA, Laidlaw MJ, Katabuchi M, Kitching RL. Identifying indicator species of elevation: Comparing the utility of woody plants, ants and moths for long-term monitoring. Austral Ecol.2015.doi:10.1111/aec.12291

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C. Scale effects and human impact on the elevational species richness gradients. Nature. 2008;453:216–20.

Philpott SM, Perfecto I, Armbrecht I, Parr, CL. Ant Diversity and Function in Disturbed and Changing Habitats.In: Lach, L, Parr, CL, Abbott, KL, editors. Ant Ecology. Oxford University Press, Oxford;2010.p. 137–156

Queiroz ACM, Ribas CR, França FM. Microhabitat Characteristics that Regulate Ant Richness Patterns: The Importance of Leaf Litter for Epigaeic Ants. Sociobiology. 2013;60: 367-373.

Rahbek, C. The role of spatial scale and the perception of large-scale species-richness patterns. EcolLett. 2005;8: 224–239.

Ribas CR, Schoereder JH, Pic M, Soares SM. Tree heterogeneity, resource availability, and larger scale process regulating arboreal ant species richness. Austral Ecol. 2003;28: 305–314.

Safford HD. Brazilian Páramos I. An introduction to the physical enviroment and vegetation of the campos de altitude. J Biogeogr. 1999;26: 693-712.

Sanders NJ. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography [R].2002;25; 25–32.

Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Glob EcolBiogeogr.2007;16: 640–649.

Stevens GC. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat. 1992;140: 893–911.

Sundqvist MK., Sanders NJ, Wardle DA. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu Rev EcolEvol Syst. 2013;44, 261–280.

Tello JS, Myers JA, Macía MJ, Fuentes AF, Cayola L, Arellano G, Loza MI, Torrez V, Cornejo M, Miranda TB, Jørgensen PM. Elevational Gradients in β-Diversity Reflect Variation in the Strength of Local Community Assembly Mechanisms across Spatial Scales. PLoS One. 2014. doi:10.1371/journal.pone.0121458

von Humboldt A. Aspects of Nature, in Different Lands and Different Climates; with Scientific Elucidations.Transl. EJ Sabine. London: Longman, Brown, Green, Longmans, John Murray. 1849;2: 347 pp.

ARTIGO 2

TEMPERATURE INFLUENCES ANT SPECIES RICHNESS PATTERNS AND SPECIES TURNOVER IN A TROPICAL ELEVATIONAL GRADIENT

Preparado de acordo com as normas da revista PLoS One

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ABSTRACT

Elevational gradients are ideal to test ecological theories and they might help in the understanding of diversity patterns. However tropical mountains are different from temperate mountain since highlands species cannot shift their ranges upward in response to climate warming. Here we evaluated ant species richness and beta diversity mechanisms across elevation relating those patterns to environmental and climatic factors. We sample ants using pitfalls traps and winkler extractor at Itatiaia National Park in an elevational gradient ranging from 600 to 2457 m a.s.l. Our results pointed out a monotonic decline pattern on α and ɣ components across the elevational gradient but no pattern for β. The main mechanism of total beta diversity across elevational bands is caused by the turnover. The greater elevation difference, the greater is the total species composition changes between the elevational bands and more of such change is due to turnover of species. Those variations can be explained by climatic factors which are linked to the gradient. We suggest that perhaps temperature acts on ants'sforaging, development, also selecting ant species in some elevations bands as a climatic filter as well. We suggest that the rapid global warming caused by anthropic actions might interfere in the process of species ranges and number since its patterns is strongly influenced by temperature.

Keywords: Altitudinal gradients. Beta diversity. Range shifts. Ecological factors. Climate change.

INTRODUCTION

Understanding patterns of species distribution have been the main objective of many ecologists and biogeographers and assessing its determining factors may help the ecological knowledge application on the maintenance of global biodiversity (Gaston, 2000). In this context, elevational gradients are ideal to test ecological theories (Colwell et al, 2008). Such quality is due to the great variability of the environment at a small spatial scale (Körner, 2007). Moreover, elevational gradients patterns are a mirror of latitudinal patterns (Rahbek, 2005) and help understanding the high spatial scales patterns and processes (Sundqvist et al., 2013). Also, at those gradients, both historical and proximate factors are shaping the cotemporary species distribution due to its well established ecological patterns (Rahbek, 2005; Colwell & Rangel, 2010) and they are appropriated to assess the global climate changing consequences on diversity (Colwell et al., 2008; Colwell & Rangel, 2010).

Studies of species richness of different taxa in elevational gradients have presented different patterns on species richness such as unimodal curve (50%), monotonic decline (25%), and other more complex patterns (25%) (Rahbek, 2005). These patterns are related to the temperature, interaction of temperature and precipitation, the availability of area, and the mid domain effect (Rahbek, 2005; Dunn et al., 2007; Romdal & Grytnes, 2007; Nogués-Bravo *et al.*, 2008; Sundqvist et al., 2013). Although the species are commonly reported as being more influenced by the temperature, we must take into account that the interaction between abiotic and biotic factors probably shapes the diversity along elevational gradients (Sundqvist et al., 2013). For example, productivity is generally negatively related to elevation (Nogués-Bravo *et al.*, 2008), and consequently to the climate, since plant biomass and net primary production (NNP) experience this changes across the gradient (Whittaker, 1960).

The variation of species community across elevations bands have importance on determining species ranges and how they are influenced by environmental factors, leading us to predict consequences Earth's global warming (Parmesan, 2006; Colwell & Rangel, 2010). Also, by understanding how the species turnover occurs along and between gradients help us to know about ecological systems sensitivity to environmental changes (Fitzpatrick et al., 2013). Taking this into account, the β diversity partitioning (Baselga, 2010) has the advantage to disentangle the mechanisms behind of species community changes. There are two mechanisms of species community changes: turnover and nestedness. The turnover of species is related to the replacement of species between sites and is commonly related to the factors that promote species endemism in consequence of historical constraints or spatial features (Qian et al., 2005; Baselga, 2010). Nestedness is related to the gain or loss of species between sites as a consequence of extinction and colonization process due to disaggregation of community by an environmental factor (Gaston & Blackburn, 2000; Baselga, 2010).

The mechanisms of β diversity is poorly explored on tropical mountains, Bishop et al. (2015) were the first to assess it on tropical mountains. But there is still a lack of knowledge about the influence of environmental and climatic factors at beta diversity mechanisms in an elevational gradient. Therefore, to understand which mechanisms of β diversity operates that may help to assess the species distribution patterns (Bishop et al., 2015) and assess which factor is promoting those changes in mountains may elucidate what structured species' ranges. Furthermore, tropical mountains gradients have a particular answer to climate change since, different of temperate mountains, the species ranges is well marked and there are endemic species on the top that cannot shift their ranges in response to climate change, leading them to extinction (Colwell et al., 2008).

In this sense, this study will access the patterns of diversity across a tropical elevational gradient, trying to understand some of the promoting factors and mechanisms. To do so, we used ants as an indicator of elevational changes since they are well distributed in tropical areas (Moreau & Bell, 2013), sensitive organisms to changes on environment (Philipott et al., 2010) and they have been well used in elevational gradients studies (e.g. Fisher, 1996; 2002; Sanders, 2002; Sanders *et al*., 2003; Longino&Collwell, 2011; Bharti *et al*., 2013; Bishop *et al*., 2014; Bishop et al., 2015). Such organisms are strongly influenced by temperature (Sanders et al., 2007; Bishop et al., 2014) likewise by habitat features as habitat heterogeneity and resources availability (Ribas et al., 2003, Costa et al., 2011 Bharti et al., 2013; Queiroz et al., 2013). We hypothesized that environmental and climate factors together drive ant diversity. Also climate factors are responsible for selecting species not allowing them to spread their ranges to all elevational gradients. We answered these questions regarding ant alpha, beta and gamma diversity on a tropical mountain: (i) How do alpha, beta and gamma diversities of an elevational band vary through the elevational gradient? (ii) Which is the main mechanism behind beta diversity across elevational bands (iii) and how does beta diversity across elevational bands and its main mechanism relate to elevation differences? (iv) Are those patterns (questions i and iii) related to environmental and climatic factors?

MATERIAL & METHODS

Study area

The sampling was conducted from February to March of 2015 (rainy season) at Itatiaia National Park (INP), in the southeast of Brazil (between 22º16’ - 22º28’ S and 44º34’ - 44º42’ W). INP was established in 1937 and it is the oldest national park in Brazil inserted in Atlantic Rain Forest biome. The park is located in Itatiaia Massif, on the highest portion of Mantiqueira Mountain. The protected area starts at 600 m elevation and it peaks at 2.878 m.

We chose eight elevations (at 600, 848, 1134, 1515, 1810, 2000, 2200 and 2457 m a.s.l) (Fig. 1), all of those were forest habitats of natural vegetation that consisted in the combination of primary and secondary forest. The park also presents high altitudinal fields at higher 2000 m a.s.l., however there is still some forest remnants in the field and we sampled only in forest formations.

Those elevations were spatially separated by at least 1.4 km.

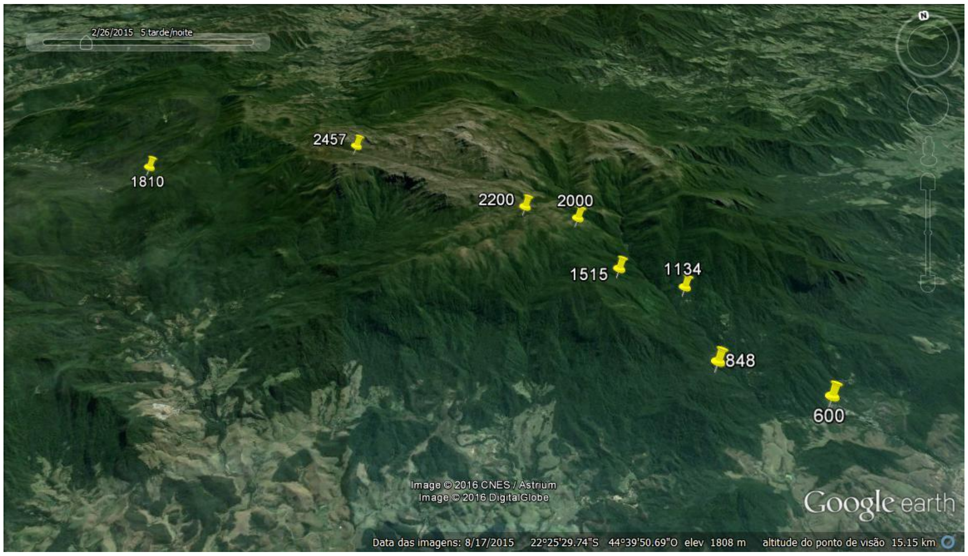


Figure 1. Transects sampling design with respective altitude values.

Ant sampling

In each elevational band we set a 200 m transect with 10 sampling points, 20 m apart from each other. We set a 1.5 m x 1.5 m grid of four unbaited pitfall traps and we sampled 1 m² of forest litter using the Fisher (1998) “miniWinkler” extractor in all sampling points (modified of Bestelmeyer et al., 2000). Pitfalls were 8 cm in diameter and 12 cm in depth, filled with a 200 ml solution of water, salt (0.4%) and liquid soap (0.6%) (Canedo-Júnior et al., 2016). They remained operating for 48 hrs in the field. Ants were extracted during 72 hrs in the “miniWinkler” sacks. We separated the morphospecies until species using auxiliary keys (Bolton, 1994; Palacio &Fernández, 2003). The voucher specimen were deposited at the Laboratório de Ecologia de Formigas at Universidade Federal de Lavras.

Environmental and climatic factors

At each sampling point we measured the environmental factors determining a 3 m radius circle. Inside it, we measured the litter leaf depth (LD), heterogeneity (LH) and dry weight (LDW) and the depth of fine roots (FRD). We stared by putting a nine liter pail (25 cm at top diameter, 20 cm bottom diameter and 23 of height) upside down on the ground of litter leaf. Then we marked the pail top diameter (25 cm of diameter) on litter leaf to collect the samples of litter and fine roots. We measured on the field the depth of litter leaf and fine roots separately by removing it from the ground and putting it inside the pail were we measured its values with a cm ruler. After that, we took the litter sample to the laboratory to calculate the litter heterogeneity and dry weight. We counted the number of different items (e.g. leaves, twings, seeds, flowers, etc.) and then we calculated the heterogeneity by the Simpson index (Queiroz et al, 2013). Then, we took the litter to the kiln-dried for 144 h at 60 °C to obtain its dry weight.

We also obtained the climatic factors as the mean annual temperature (MAT) and mean annual precipitation (MAP) for each elevation from GIS data layers (30 arc-seconds) of the WorldClim 1.4 database (Hijmans et. al., 2005).

Since the WorldClim computes the data based on elevation, we had one of those measures per transect (elevation). However, the WorldClim data has shown to be an appropriate tool for cloud forest in a sort of mountains (Jarvis & Mulligan, 2011).

Data analyses

To answer our first question related to alpha, beta and gamma diversity per elevation, we performed the multiplicative partitioning of diversity ($\beta = \gamma / \alpha$) (Whittaker, 1960) to extract the diversity components (α, β and ɣ) per elevation. The α value is the mean species richness per pitfall trap in a transect. Since we had 10 sampling points per transect (elevation), β value can vary from one to 10 different ant communities in terms of species richness. The ɣ value is the overall species richness per transect (elevation). First, to investigate if α, β and ɣ diversity components relate to elevation by a monotonic decline or hump-shaped function we modified the Nagai (2011) function to generate linear and quadratic models for comparison from those diversity components. Using Akaike's information, we verified which model is more appropriated, using the corrected Aikaike's criteria (AICc) which indicates the best model (Burnham et al., 2011; Motulsky & Christopolus, 2003). We considered the best model the one which obtain the lowest AIC value. Second, we performed generalized linear models (GLMs) with those diversity components as response variables and the elevation as explanatory variable. The analyses were performed with Gaussian distribution for α and β components and with Poisson distribution for γ component. We did a residual analysis to verify the adequacy of error distribution (Crawley, 2002).

To answer our second question related to the beta diversity across the elevational gradient, we performed the beta diversity partition proposed by Baselga (2010). The overall beta diversity ($\beta_{sor)}$can be additively partitioned in two components; turnover ($\beta_{sim)}$ and nestedeness-resultant (β_{sne}). The β_{sim} is derived by the Simpson dissimilarity index and it reflects the beta diversity relative to the turnover of species. The β_{sne} refers to a nestedness-resultant dissimilarity from the β_{sor} and β_{sim} calculation (Baselga, 2010). Therefore, we partitioned total beta diversity to verify which one is the main mechanism behind the change of species across elevations (turnover or nestedeness). To answer our third question, and verify how total beta diversity (β_{sor}) and its main mechanism (β_{sim} or β_{sne}) are related to elevation difference between transects we calculated the pairwise metrics (β_{sor} and β_{sim} or β_{sne}) always extracting its values between the lowest elevation and the others seven higher elevations (one by one). After that, we created GLMs using those two pairwise metrics as response variable and as the explanatory variables the elevation differences resulted from the difference of the lowest elevation to the others seven elevations (one by one) in which we extracted the two β pairwise metrics. The analyses were performed with binomial distribution and we also assessed it by a residual analysis to verify the adequacy of error distribution (Crawley, 2002).

To assess which environmental and climatic factors are involved with the diversity patterns of the elevational gradient, first we verified if there was collinearity between the variables using Spearman distance, including the elevation to not confound the factors that are actually linked to the gradient. Secondly, we constructed generalized linear models (GLMs). We used as response variables, α, β and ɣ (referent to our first question) and β_{sor} andβ_{sim} or β_{sne} (referent to our second question) and the explanatory variables are the environmental and climatic factors. The α and β values were related to the mean of environmental factor values per transect while ɣ was related to the sum of environmental factor values per transect. We choose this approach because since α and β are calculated as mean number of species we correlated them with mean values of factors and the sum of factors for ɣ since it is the total number of species.

After that, to assess which factors are involved with beta diversity related to elevation differences (β_{sor}, β_{sim} or β_{sne}), we used the average values of the environmental and climatic factors per transect as explanatory variables. We used the difference of those environmental and climatic factors from the lowest elevation to the others seven higher elevations (one by one). The entry order of explanatory variables in the model was chosen by the order of the highest F value to the lowest. The analyses were performed with Gaussian distribution for α and β component, Poisson distribution for ɣ component and binomial distribution for β_{sor},β_{sim} and β_{sne};all GLMs were submitted to a residual analysis.

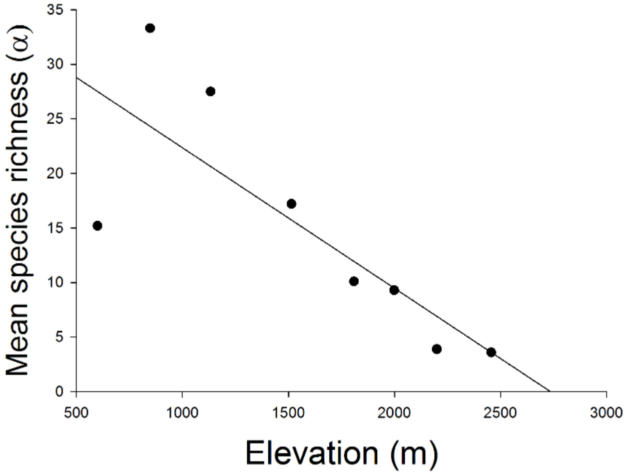
RESULTS

We collected 263 ant morphospecies, 162 from pitfall traps and 181 from “miniWinkler” extractor. The morphospecies belong to 47 genera, which the most specious genera were *Pheidole* (39), *Solenopsis* (30), *Hypoponera* (24), *Brachymyrmex* (22) *Camponotus* (17) and *Wasmannia* (17).

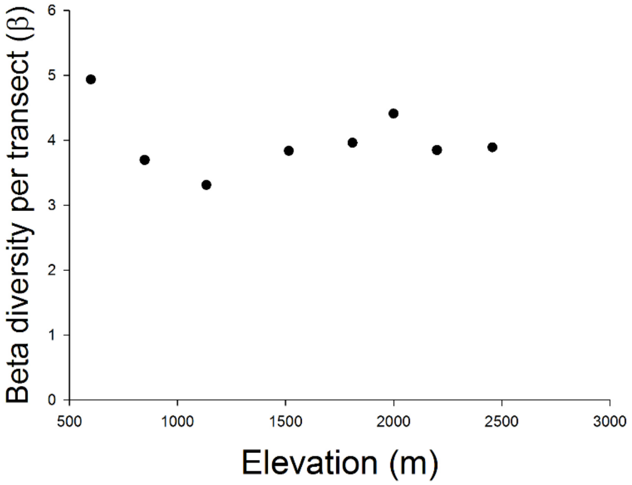
Elevational patterns

Both α, β and ɣ follow better a linear than a quadratic function (Supplementary material, Fig. 1). The α diversity (F =10.44; *p* = 0.018) and ɣ diversity (F = 19.02; *p* = 0.004) decreased with elevation (Fig 2a and 2b). However the β diversity did not varied with the elevational gradient (F = 0.196; *p* = 0.673) (Fig 2c).

a)


Mean species richness (α)
35
30
25
20
15
10
5
0
500
1000
1500
2000
2500
3000
Elevation (m)

b)


Beta diversity per transect (β)
6
5
4
3
2
1
0
500
1000
1500
2000
2500
3000
Elevation (m)

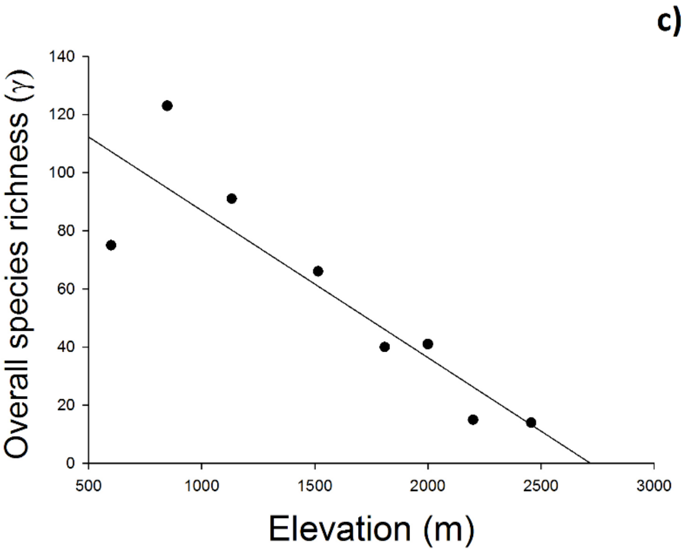


Figure 2. Relationship between diversity components per transect with elevation. a) Mean of ant species richness in a sampling point per transect (α) (F =10.44; *p* = 0.018; n = 8). b) Beta diversity per transect (β= γ /α) (F = 0.196; *p* = 0.673; n = 8). c) Overall species richness per transect (ɣ) (F = 19.02; *p* = 0.004; n = 8). Points are the values of diversity components and the line is the function of the data.

In relation to the partitioning of the total beta diversity across all elevational bands, the turnover (β_{sim}) was pointed out as the main mechanism being the component β_{sor} (mean value = 0.79) composed by 85% of β_{sim} (mean value = 0.67) and 15% by β_{sne} (mean value = 0.12). Therefore, we used only β_{sor} and β_{sim} to assess the effect of elevation difference. The greater the elevation difference, the greater is the total beta diversity (β_{sor}: Fig. 3a)(F = 43.73; *p* = 0.001) and the species turnover (β_{sim}: Fig. 3b) (F = 17.17; *p* = 0.009).

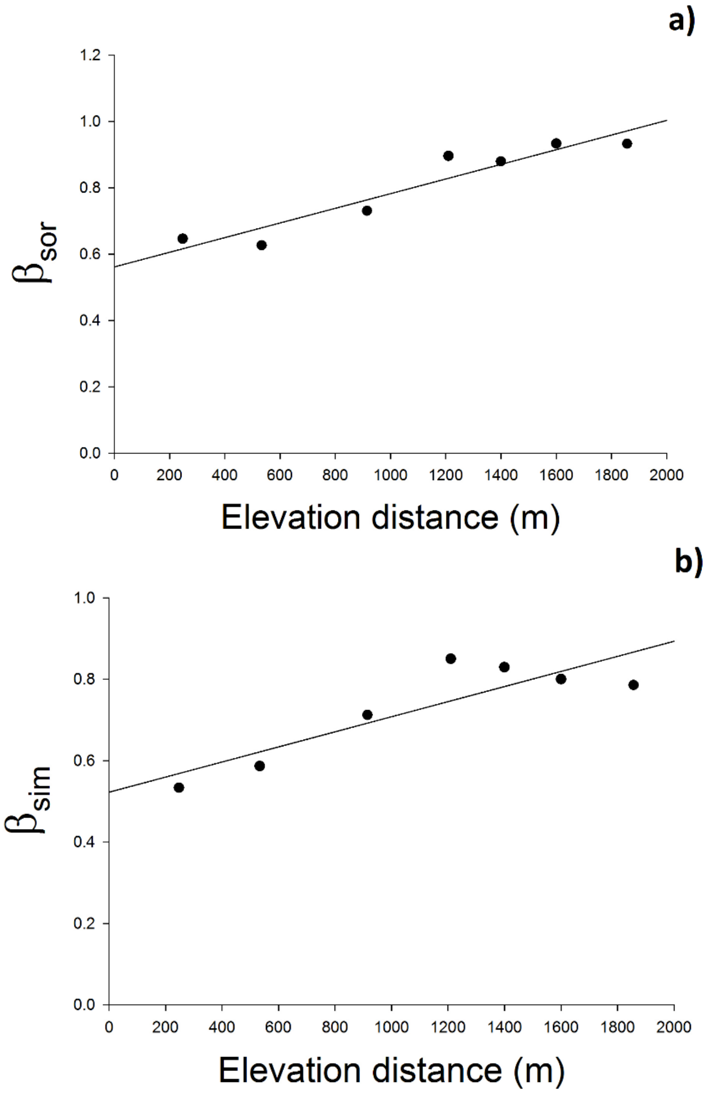
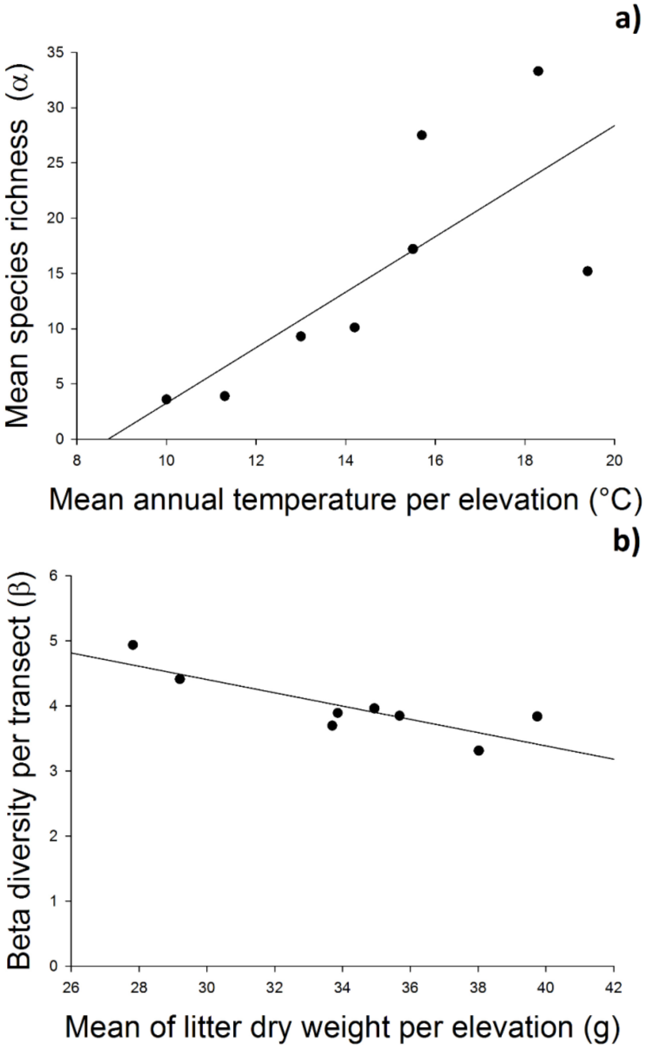


Figure 3. Relationship between two pairwise metrics of beta partitioning between the lowest elevation and the other seven higher elevations counter the elevation distance between the correspondents transect. a) Total beta diversity (β_{sor}) of species between the elevation distances (F = 43.73; $p = 0.001$; n = 7). b) Difference of species caused by turnover (β_{sim}) between the elevation differences (F = 17.17; $p = 0.009$; n = 7). Points are the values of two pairwise metrics and the line is the function of the data.

Influence of environmental and climatic factors

Since the annual mean temperature (MAT) and the annual mean precipitation (MAP) were correlated ($r^2 = -0.98$), we decided to use only the MAT in the model because the temperature is directly related to the elevational gradient and MAP varies according a regional influence (Körner, 2007) (Table 1. Supplementary material). Also fine roots depth (FRD) correlated with litter depth (LD) ($r^2 = 0.97$) (Table 1. Supplementary material) so we decided to use only FRD because we believe that litter features are yet well represented by others variables. Only MAT and MAP were correlate with elevation ($r^2 > 0.75$). In this sense, only those variables are actually linked to elevational gradient of our study.

The α diversity was positively influenced by MAT (F = 8.12; $p = 0.029$) (Fig. 4a), but litter heterogeneity (LH) (F = 4.08; $p = 0.113$), litter dry weight (LDW) (F = 0.20; $p = 0.683$) and FRD (F = 0.41; $p = 0.549$) did not influenced α diversity. The beta diversity per transect(β) decreases with the increasing of LDW (F = 14.51; $p = 0.009$) (Fig. 4b), but it was not influenced by MAT (F = 0.19; $p = 0.691$), LH (F = 0.01; $p = 0.936$ and by FRD (F = 0.08; $p = 0.783$). The overall species per elevation (ɣ) was positively influenced by MAT (F = 41.36; $p = 0.001$) (Fig. 4c) and LH (F = 10.53; $p = 0.022$) (Fig. 4d) (since Simpson index we looked by inverse, as values nearest from 0 indicates less heterogeneous litter), but not by LDW (F = 0.04; *p* = 0.848) and FRD (F = 7.11; *p* = 0.055).



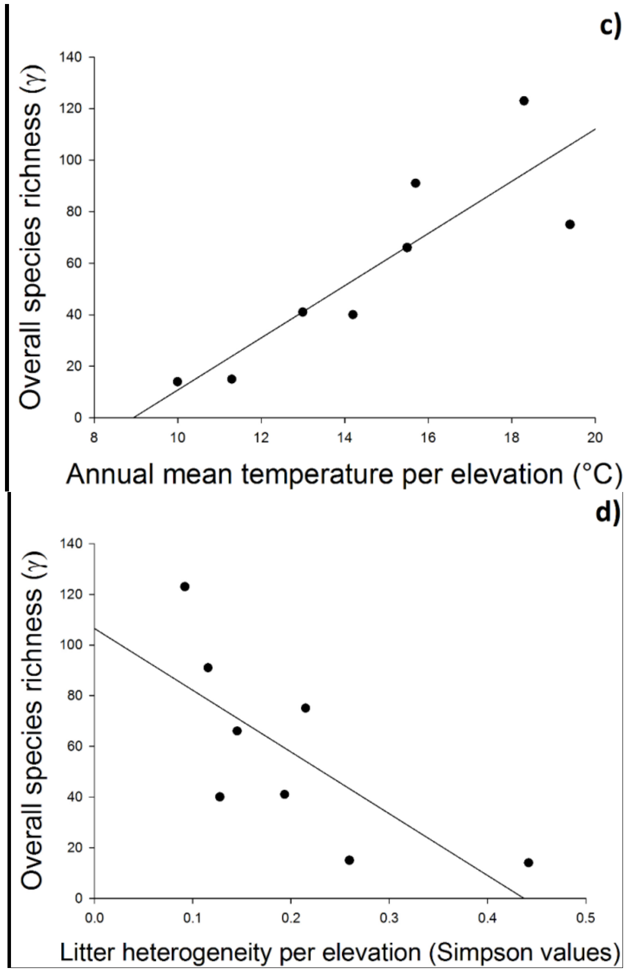


Figure 4. Relationship between diversity components α, β and ɣ with environmental and climatic factors. **a)**relationship of mean of ant species richness of the sampling point per transect (α) with the mean annual temperature (MAT) (F = 8.12; *p* = 0.029; n = 8). **b)**relationship of difference of sampling points species within transects (β) with the mean of litter dry weight (LDW) per transect (F = 14.51; *p* = 0.009; n = 8). **c)**relationship of overall species per elevation (ɣ) with mean annual temperature (MAT) (F = 41.36; *p* = 0.001; n = 8). **d)**relationship of overall species per elevation (ɣ) with litter heterogeneity (LH) per elevation indicated by the Simpson index values (F = 10.53; *p* = 0.022; n = 8), where values nearest from 0 indicates less heterogeneous litter. Points are the values of diversity components per transect and the line is the function of the data.

The total species composition changes (β_{sor}) increases when the MAT difference between elevations bands increases (F = 19.35; *p* = 0.007) (Fig. 5a). However, LH (F = 2.47; *p* = 0.214), LDW (F = 2.08; *p* = 0.285) and FRD (F = 3.08; *p* = 0.285) did not influenced the species exchange. The species turnover (β_{sim}) was positively influenced by the difference of MAT (F = 8.02; *p* = 0.047) (Fig. 5b) and by the difference of FRD (F = 139.36; p = 0.0003) (Fig. 6) but not by LH (F =0.56; *p* = 0.529) nor LDW (F =2.28; *p* = 0.227).

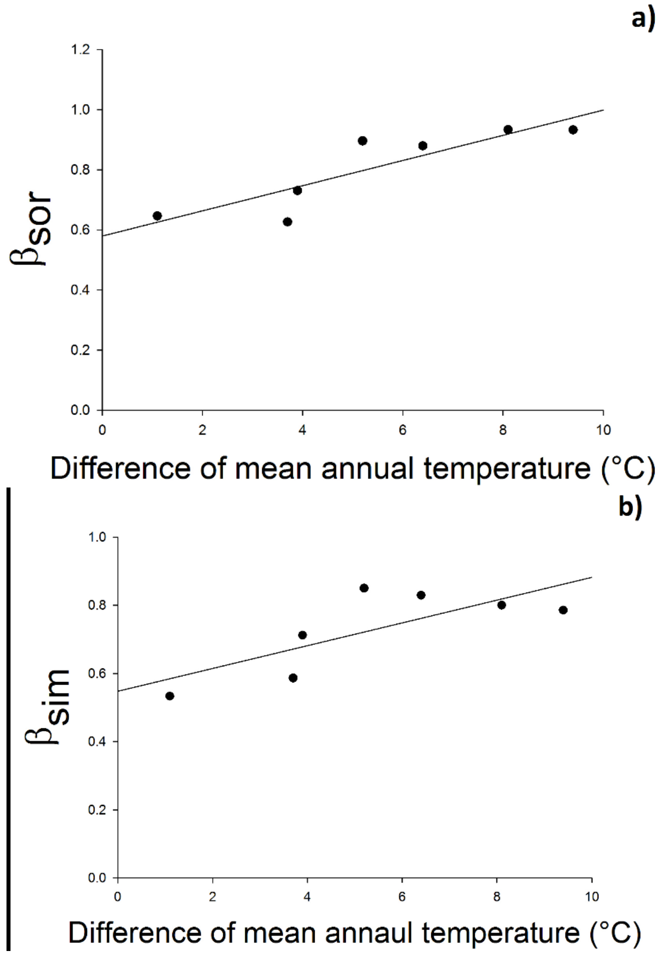


Figure 5. Relationship of total beta diversity (β_{sor}) and its main mechanism (β_{sim}) with the differences of climatic factors of its respective elevation differences. **a)**relationship of β_{sor} and the difference of mean annual temperature (F = 19.35; *p* = 0.007; n = 7). **b)**relationship of turnover component (β_{sim}) with the difference annual mean temperature (F = 8.02; *p* = 0.047; n = 7). Points are the pairwise values of β_{sor} and β_{sim} extracted between the lowest elevation (600 m) and the other seven highest and the line is the function of the data.

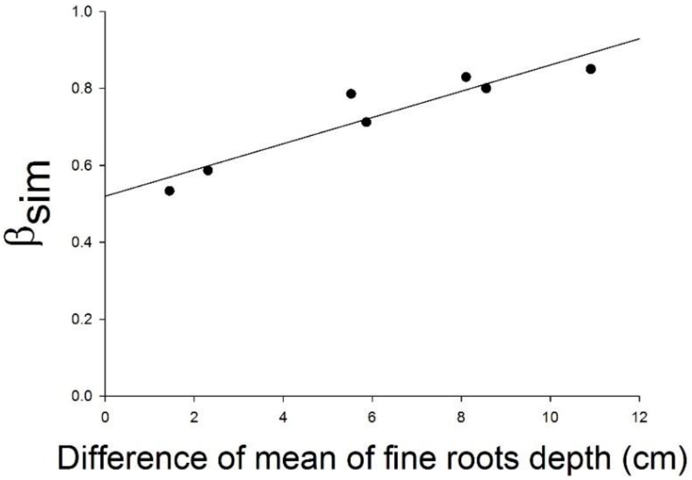


Figure 6. Relationship of total beta diversity main mechanism (β_{sim}) with the differences of environmental factorof fine roots depth (FRD) (F = 139.36; p = 0.0003; n=7). Points are the pairwise values of βsim extracted between the lowest elevation (600 m) and the other seven highest and the line is the function of the data.

DISCUSSION

This work represents one step further on tropical elevational gradient studies since it assessed not only the diversity patterns (α, β and ɣ diversities) and their influencing variables but also verified the changes on species composition between elevations differences, identifing the possible causal processes and assessing which environmental and climatic factors are behind it. Our results pointed out a monotonic decline pattern on α and ɣ components across the elevational gradient but no pattern for β. Temperature and environmental factors (linked to litter) influenced those patterns. However, environmental factors are not linked to elevational gradient, so it reflect only the spatial variation of those factors. The greater elevation difference, the greater is the total species composition changes between the elevational bands and more of such change is due to turnover of species. Once more, temperature and one environmental factor influenced the species changes across elevations and their ranges, since those variables explain the species turnover across the elevational gradient.

Elevational Patterns

It is not a surprise that α and ɣ presented the same monotonic decline pattern because the regional species pool has a direct influence on local species richness (Ricklefs, 2015). Our results are according to some studies (Bhrulet al., 1999; Lessard et al., 2007 Sanders et al., 2007) but differed from others (Fisher, 1998; Sanders, 2002; Longino& Colwell, 2011; Bishop *et al*., 2014) that found a hump-shaped pattern. The monotonic decline is not the most common pattern, but the hump-shaped (Rahbek, 2005). Maybe our results is a reflect of not sampling the whole gradient (since sea level), as proposed by Rahbek (2005), where the whole gradient assumed a hump-shaped form. Nogués-Bravo and colleagues (2008) argued that length extent of the gradient may switch the observed patterns (monotonic and hump-shaped) depending on the omission of the lowers transects, which produces a monotonic pattern. Also, patterns on elevational gradients depends on the grain size and extent length of gradient as well (Rahbek, 2005). However, we believe that our grain size (0.2 km) and extent length of gradient (1840 m) are not causing the monotonic decline. In accordance with our beliefes, Nogués- Bravo and colleagues (2008) noted that grain size did not interfere on the changes of those patterns and highlights that the hump-shaped is not a universal pattern on elevational gradients, but excluding or maintaining lowers elevations in the analysis, which are often influenced by anthropic actions, it can bias toward a monotonic pattern. Such anthropic disturbance at lowlands is present in our study as well and it may reflect indirectly on the low values of both α and ɣ of our first elevation. Although that transect was set in a protected area, our first elevation presented many exotic plants species that we could not find over all the gradient and such degree of anthropization maybe resulted in those low values of diversity. In summary, we believe that the monotonic pattern found in our study is due the fact that we did not sampled the complete gradient (since sea level) since Itatiaia Massif start at 300 m a.s.l. and the protected area at 600 m a.s.l.. However, probably such pattern might is reflecting a strong relationship with some factor that covary with elevation (see below).

The beta diversity inside each elevational band did not vary across the gradient. Considering that beta diversity is usually influenced by the habitat heterogeneity of resources and conditions, it is not necessarily related to the elevational variation. In other words, the beta diversity of each elevation may be driven by the habitat heterogeneity of the correspondent transect and it does not need to vary across the gradient. However the beta diversity of our lower elevation presented the highest value compared to the others. We believe that perhaps it occurred due the degree of anthropization presented at such elevation. Basing in that, we performed the same analyses excluding our lower elevation but we observed the same, the absence of a pattern. It lead us to suggest that the same mechanisms acting on beta diversity within a elevational band occur at lowlands and at highlands, taking into account the intrinsic environmental factors as habitat variation and the pool of species of the transects.

The total beta diversity of our gradient is driven mainly by the spatial turnover of species (85%). We believe that it might be a result of some climactic filter at elevational bands in PNI gradient. Bruhl et al. (1999) have argued that ant species present a narrow range of distribution in tropical mountains resulting in high levels of turnover between the gradient. As Itaiaia Massif presents well defined climatic zones (Segadas-Viana & Dau, 1965) and ant species ranges are limited by climate (Geraghty et al., 2007) maybe the total beta diversity of ant species is due the changes at those climate zones. Consequently, there might be a climatic filter that allows only ants species which is adapted to their specifically climate zones at some elevational band, resulting in species turnover along the gradient instead a gain or loss species caused by nestedeness.

We found that the increase of elevation difference is according the increasing of total species composition changes (β_{sor}), and also of its driven mechanism, the spatial turnover (β_{sim}). The same pattern with elevation was reported in others studies (Wang et al., 2012; Bishop et al., 2015). Bishop and colleagues (2015) pointed out that species tend to specialize at specific ranges instead of occurring at whole elevation and it highlights the importance of maintaining the whole mountain biodiversity since the species occupy different elevational bands. Before that, Fisher (1996, 1998; 1999; 2002) was the first to document that tropical mountain ant community is composed by two distinct communities, one from lower and other from higher elevations, which presented high levels of turnover at mid elevations. Based in that, we can also observe that β_{sor} values at lower elevations are more similar as well higher elevations are between them but there is a more pronounced difference between β_{sor} values of lowers and higher elevations. Considering the small spatial scale of a mountain, probably the dispersion of species is not a limiting process that avoid the species to achieve all the mountain places. However, even though ant species are able to disperse to all gradient, we suggest that ant species are filtered by climatic factors because despite they can disperse, not all species are able to colonize some elevations. In this sense, we suggest that the spatial turnover of species is higher when elevation difference is higher probably due the climatic differences that also increase with elevation difference.

Influence of environmental and climatic factors

The α and ɣ relationship with elevation are influenced by MAT. Those results are conforming to a range of studies (Bhrul *et al*., 1999; Sanders *et al*., 2007; Longino & Colwell, 2001; Bishop et al; 2014). Litter heterogeneity (LH) also positively influenced ɣ diversity. This environmental factor is linked to availability of ant's different food and nesting resources (Queiroz et al., 2013). However, besides LH influenced ɣ diversity, such factor did not correlated with elevation. In this sense, the elevational gradient in species richness founded in our study should be caused by temperature.

The temperature influences ants activity, and so itvaries according elevational gradient. According species-temperature hypothesis (Sanders et al. 2007) such climatic factor may be correlated with net primary productivity (NPP), and acts limiting species physiology, range and behavior of individuals and also is related to the speciation rates. Bhrul et al. (1999) attributed the decline of species in relation to elevational gradient to the fact that depending of temperature level, lower values may compromise ant's foraging and its larvals' development. In this sense, we believe that the pattern found in this study is due the fact that there are few species that can maintain its colonies at low levels of temperature at highlands.

Although beta diversity did not vary with elevation, it was related with the LDW. It has been documented the influence of such factor on ant species richness, because such factor is a measure of resource availability (Queiroz et al., 2013). Maybe high levels of resources at such spatial scale (transect) homogenize ant communities, allowing the species to nest and forage at the whole transect and thus decreasing the difference between ant communities within transect when increasing amounts of litter. Furthermore, maybe the absence of an elevational gradient in beta diversity is due its influencing factor (LDW) did not covary with elevation.

We found that when increasing elevation difference, so does the total species composition changes (β_{sor}) and such pattern is explained by MAT. In the same way, the pattern of spatial turnover (β_{sim}) according to elevation differences is also explained by MAT. However, the spatial turnover (β_{sim}) is also explained by FRD that is not linked to elevation. It has been documented that the turnover of plants in a latitudinal and longitudinal gradient approach is influenced by both environmental and climatic factors (Qian et al, 2005). Although the fine roots are documented for maintaining about 50% of the annual primary productivity allocated on belowground (Burke & Raynald, 1994) and also that its mass varies on a tropical elevational gradient as well (Souza Neto et al., 2011), such factor is not correlated to elevation in our study. Maybe great differences of FRD in habitat my produce different conditions to ants since such factor is a layer separating soil from litter leaf, and also act as resources since it might provide nesting places for ants. Thus, we suggest that the difference in the amount of FRD might increase the ant species turnover, but not causing an elevational gradient in species turnover since FRD is not correlated to elevation.

The influence of MAT on both β_{sor} and β_{sim} highlights that probably such factor actually acts as a climatic filter in our elevational gradient. For plant species, climatic factors are an important structuring the range that species occur in the elevational gradient. Taking into account that the dispersal spatial scale is not a limiting process, maybe the species of lowlands are not able to spread their ranges at high elevations because they are not adapted at lowers values of temperature, since we observe a gradual decrease of temperature according the elevation difference. Thus, we observe a substitution by species that is lower temperature tolerant over and over according the increasing of elevational bands.

However, observing those results, a question is still not answered: How are ant species gradually replaced along the whole gradient? What processes are behind it? Taking into account the influence of temperature on the species turnover, and the oscillation of temperature at glacial and interglacial periods, we also suggest that the replacement of species across elevation may be a reflect of such variation of temperature between those periods that leaded lowland species ranges to upward and vice versa. Longino & Colwell (2011) pointed out that in an tropical elevational gradient, the Brava Transect, lowland species ranges is broader than highland species ranges as a reflect of the natural recent interglacial warming and possibly ant species shifted their ranges up and down during glacial and interglacial periods at Pleistocene. Also, the authors argued that probably ant species in that tropical mountain is limited by a critical thermal minima (which value decline with elevation) instead of a critical thermal maxima (which values changes subtly with elevation). Such mechanism was observed after in some ants species that shifted their ranges and were limited by critical thermal minima in elevational gradient (Warren & Chick, 2013). In others words, highlands tropical ant species might tolerate warmer temperatures than they experience nowadays, in other hand, lowland species are limited by cold temperatures (Longino & Colwell, 2011). Hence, in the interglacial periods, when the temperature got warmer, maybe the species range upward to highlands but at glacial periods they turned back to down. In this process, from highlands to lowlands, maybe only species that tolerate colder temperatures were able to still exist at those elevational bands and so it maybe reflects on the gradual species turnover observed in this study.

Main conclusions

Here we verified that not only ant species richness is driven by temperature, but also its turnover across a tropical mountain gradient. Such factor had a fundamental importance on diversity patterns since the decreasing of its levels leads species richness to decline and also, the higher temperature difference across elevational bands, the higher is the turnover of species. Since elevational gradients are appropriate for climate-changing studies (MacCain & Colwell, 2011), these finds may clarify some possible impacts of global warming. Taking into account the susceptibility of ant species patterns to temperature, the effects of a rapidly warming of the climate might compromise it.

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REFERENCES

Baselga A. Partitioning the turnover and nestedness components of beta diversity. Glob EcolBiogeogr. 2010;19: 134–143.

Bestelmeyer BT, Agosti D, Leeanne F, Alonso T, Brandão CRF, Brown WL, Delabie JHC, Silvestre R. Field techniques for the study of ground-living ants: An Overview, description, and evaluation, p. 122-144. In.: Agosti D, Majer JD, Tennant A, Schultz T editors., Ants: standart methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, 2000. pp. 280.

Bharti H, Sharma Y, Bharti M, Pfeiffer M. Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas. Asian Myrmecol. 2013;5: 79–101.

Bolton B. Identification guide to the ant genera of the world. Cambridge, Harvard University Press, 1994. pp. 222.

Bhrul CA, Mohamed V, Linsenmair KE. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. J Trop Ecol. 1999;15: 265–277.

Bishop TR, Roberterson MP, van Resenburg BJ, Parr CL. Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. J Biogeogr.2014;41: 2256–2268.

Bishop TR, Robertson MP, van Rensburg BJ, Parr CL. 2015. Contrasting species and functional beta diversity in montane ant assemblages. J Biogeogr., doi:10.1111/jbi.12537

Burke M, Raynald DJ. Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. Plant Soil. 1994;162:135–146

Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. BehavEcolSociobiol. 2011;65:23–35.

Canedo-Júnior EO, Cuissi RC, Curi NHA, Demetrio GR, Lasmar CJ, Malves K, Ribas CR.Can anthropic fires affect epigaeic and hypogaeicCerrado ant

(Hymenoptera: Formicidae) communities in the same way? Rev Biol Trop.2016;64: 95-104.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. Science [R]. 2008. doi: 10.1126/science.1162547

Colwell RK, Rangel TF. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. Philos Trans R Soc B.,2010;365: 3695–3707.

Costa FV, Neves FS, Silva JO, Fagundes M. Relationship between plant development, tannin concentration and insects associated with *Copaiferalangsdorffii*(Fabaceae). Arthropod Plant Interact. 2011;5: 9-18.

Crawley MJ. Statistical computing: An Introduction to Data Analysis Using S-Plus. London: John Wiley & Sons, Ltd; 2002.

Dunn RR, McCain CM, Sanders NJ. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. GlobEcol Biogeogr.2007;16: 305–312.

Fernández F. SubfamiliaMyrmicinae. In: Fernández F. editor. Introducción a lashormigas de laregión Neotropical. Bogotá, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. 2003.

Fisher BL. Ant diversity patterns along an elevational gradient in the Reserve NaturelleIntegraled'Andringitra, Madagascar. Fieldiana Life Earth Sci. 1996;85:93–108.

Fisher BL. Ant diversity patterns along an elevational gradient in the RéserveSpécialed'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. Fieldiana Life Earth Sci.1998;90:39–67.

Fisher BL. Ant diversity patterns along an elevational gradient in the RéserveNaturelleIntégrale d' Androhaheta, Madagascar. In: GOODMAN, S. M. (ed), A floral and faunal inventory of the RéserveNaturelleIntégrale d' Andohahela, Madagascar: With reference to elevational variantion. Fieldiana Life Earth Sci. 1999;94: 129-147.

Fisher BL. Ant diversity patterns along an elevational gradient in the RéserveSpéciale de Manongarivo, Madagascar. Boissiera. 2002;59: 311–328.

Fitzpatrick MC, Sanders NJ, Normand S, Svenning JC, Ferrier S, Gove AD, Dunn RR. Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. Proc R Soc B.2013. doi:org/10.1098/rspb.2013.1201

Gaston, KJ. Global patterns in biodiversity. Nature. 2000;405: 220-227.

Gaston KJ, Blackburn TM. Pattern and process in macroecology. Blackwell Science, Oxford.2000.

Geraghty MJ, Dunn RR, Sanders NJ. Body size, colony size, and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's Rule?Myrmecol News. 2007;10: 51-58.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol. 2005;25: 1965–1978.

Jarvis A, Mulligan, M. The climate of cloud forests. Hydrol Process.2011;25: 327–343.

Lessard J, Dunn RR, Parker CR, Sanders NJ. Rarity and Diversity in Forest Ant Assemblages of Great Smoky Mountains National Park. Southeast. Nat.2007.doi: dx.doi.org/10.1656/1528-7092(2007)6[215:RADIFA]2.0.CO;2

Kaspari M, Ward PS, Yuan M. Energy gradients and the geographic distribution of local ant diversity. Oecologia. 2004;140:407–413.

Körner C. The use of ‘altitude’ in ecological research. Trends EcolEvol. 2007;22: 569–574.

Longino JT, Colwell RK. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. Ecosphere. 2011;2: Article 29.

McCain CM, Colwell RK. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. EcolLett. 2011;14: 1236–1245.

Marquet PA et al.Breaking the stick in space: niche models, metacommunities and patterns in the relative abundance of species. In: Blackburn TM; Gaston KJ, editors.Macroecology: Concepts and consequences. Blackwell Publishing;2002. pp. 65-85.

Moreau, C. S; Bell, C. D. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolutionof the ants. Evol.2013. doi:10.1111/evo.1210

Motulsky H, Christopolus A. Fitting models to biological data using linear and nonlinear regression. A practical guide to curve fitting. GraphPad Software Inc, San Diego CA. 2003. Available:www.graphpad.com.

Nagai ME. (2011). Available:http://ecologia.ib.usp.br/

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C. Scale effects and human impact on the elevational species richness gradients. Nature. 2008;453:216–20.

Parmesan C. Ecological and evolutionary responses to recent climate change. Annu Rev EcolEvol Syst. 2006;37: 637–669.

Philpott SM, Perfecto I, Armbrecht I, Parr, CL.. Ant Diversity and Function in Disturbed and Changing Habitats.In: Lach, L, Parr, CL, Abbott, KL. (Eds.), Ant Ecology. Oxford University Press, Oxford; 2010. p. 137–156.

Qian H, Ricklefs RE, White PS. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. EcolLett. 2005;8: 15–22.

Queiroz ACM, Ribas CR, França FM. Microhabitat Characteristics that Regulate Ant Richness Patterns: The Importance of Leaf Litter for Epigaeic Ants. Sociobiology. 2013;60: 367-373.

Rahbek, C. The role of spatial scale and the perception of large-scale species-richness patterns. EcolLett. 2005;8: 224–239.

Ribas CR, Schoereder JH, Pic M, Soares SM. Tree heterogeneity, resource availability, and larger scale process regulating arboreal ant species richness. Austral Ecol. 2003;28: 305–314.

Ricklefs RE. Intrinsic dynamics of the regional community. EcolLett. 2015.doi: 10.1111/ele.124314.

Romdal TS, Grytnes JA. An indirect area effect on elevational species richness patterns. Ecography [R].2007;30: 440–448.

Segadas-Viana F, Dau L. Ecology of the Itatiaia range, southeastern Brazil. II-Climates and altitudinal climatic zonation. ArquivoMuseuNacional, Brasil, RJ. 1965;53: 31- 53.

Sanders NJ. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography [R]. 2002;25: 25–32.

Sanders NJ, Moss J, Wagner D. Patterns of ant species richness along elevational gradients in an arid ecosystem. Glob EcolBiogeogr. 2003;12: 93–102.

Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. . GlobEcol Biogeogr.2007;16: 640–649.

Sousa-Neto E, Carmo JB, Keller M, Martins SC, L. Alves LF, Vieira1 SA, PiccoloMC, Camargo P, Couto HTZ, Joly CA, Martinelli1 LA. Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest. Biogeosciences. 2011;8: 733–742.

Sundqvist MK., Sanders NJ, Wardle DA. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu Rev EcolEvol Syst. 2013;44: 261–280.

Wang J, Soininen J, Zhang Y, Wang B, Yang, Shen, J. Patterns of elevational beta diversity in microand macroorganisms. Glob EcolBiogeogr. 2012;21: 743–750.

Whittaker RH. Vegetation of the Siskiyou Mountains, Oregon and California.EcolMonogr. 1960;30: 279–338.

CONCLUSÃO GERAL

Devido ao fato de gradientes altitudinais serem amplamente usados para testar teorias ecológicas, é importante não confundir os fatores que estão ligados e os que não estão com o gradiente. Dessa forma, teremos acesso aos fatores responsáveis pelos padrões encontrados, o que pode ajudar na compreensão da distribuição das espécies bem como a forma que esses fatores atuam sob as comunidades.

No primeiro manuscrito, foi avaliado de dois tipos de abordagens ao longo do gradiente, uma padronizando o tipo de vegetação amostrado e outro usando dois tipos de vegetação. Verificamos que as duas abordagens podem obter padrões diferentes ou não, dependendo do componente de diversidade usado. Isso pode ser devido ao fato de que as condições ambientais dos dois tipos de habitat podem tanto mudar os padrões encontrados (na diversidade alfa) quanto perder poder estatístico e diminuir o tamanho do efeito da perda de espécies ao longo do gradiente (na diversidade gama). Desta forma, aconselhamos a padronizar o tipo de formação da vegetação ao longo do gradiente amostrado para não se confundirem as influências de fatores ligados ao gradiente e fatores que mudam simplesmente pela troca do tipo de vegetação.

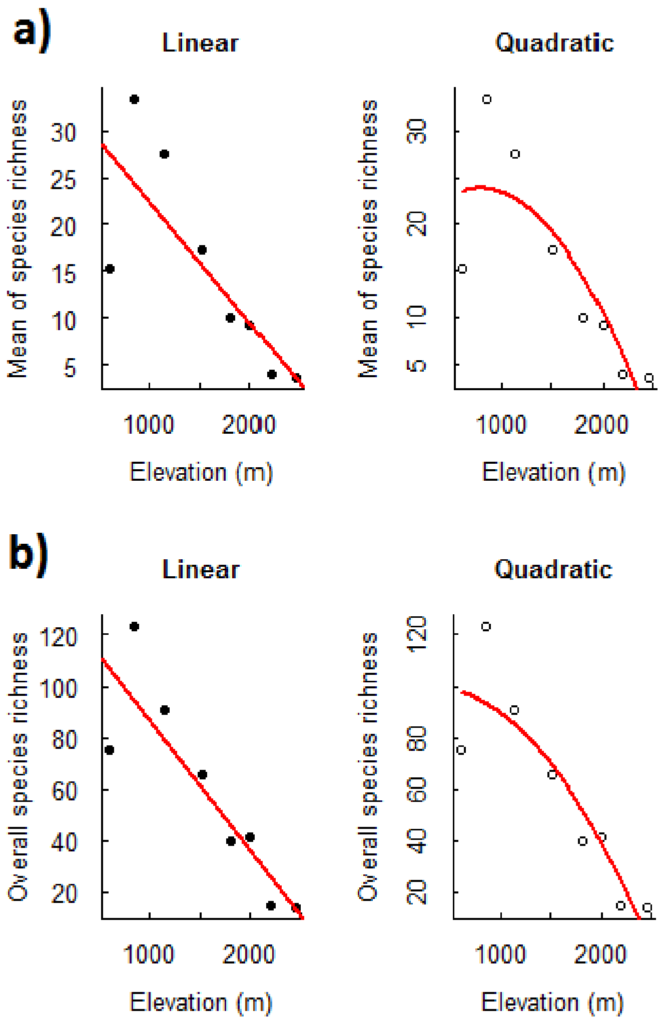
No segundo manuscrito, verificamos a forte influência da temperatura nos padrões da diversidade de formigas. Tal fator climático está ligado desde o declínio monotônico das espécies à substituição gradativa das espécies ao longo do gradiente. Possivelmente a temperatura age como determinante desse declínio por influenciar o forrageamento e desenvolvimento das formigas. E também pode atuar como filtro climático das espécies ao longo do gradiente. Dessa forma, uma mudança rápida do clima global talvez possa comprometer a fauna de formigas das montanhas tropicais comprometendo os padrões encontrados.

A presente dissertação foi um passo a mais em estudos sobre os padrões e alcance das espécies ao longo de um gradiente altitudinal. Além de ser o primeiro estudo a verificar o viés causado pela não padronização do tipo de formação da vegetação nos padrões altitudinais, também verificou que a temperatura, além de influenciar a diversidade alfa e gama, está correlacionada com a substituição das espécies ao longo do gradiente.

SUPPLEMENTARY MATERIAL

Table 1. Spearman's correlation with elevation and the measures of environmental factors: litter heterogeneity (LH), litter dry weight (LDW), litter depth (LD), and fine roots depth (FRD): and climatic factors: mean annual temperature (MAT) and mean annual precipitation (MAP). Test statistic value under diagonal.

	Elevation	LH	LDW	LD	FRD	MAT	MAP
Elevation							
LH	0.61905						
LDW	0.21429	-0.11905					
LD	0.66667	0.14286	0.071429				
FRD	0.69048	0.16667	0.14286	0.97619			
MAT	-1	-0.61905	-0.21429	-0.66667	-0.69048		
MAP	0.97619	0.7381	0.14286	0.61905	0.66667	-0.97619	


a)
Linear
Quadratic
Mean of species richness
30
25
20
15
10
5
1000
2000
Elevation (m)
Mean of species richness
30
20
10
5
1000
2000
Elevation (m)
b)
Linear
Quadratic
Overall species richness
120
100
80
60
40
20
1000
2000
Elevation (m)
Overall species richness
120
80
60
40
20
1000
2000
Elevation (m)

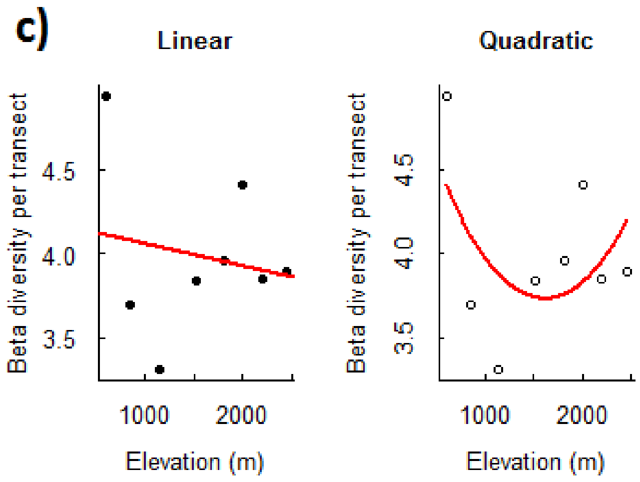


Figure 1. Comparison between linear and quadractic function by a modified method by Nagai (2011) of ant diversity components α and ɣ with elevation at Itatiaia National Park . **a)** Mean of species richness (α) and its development as a linear function (a1 = 35.25, b1 = -0.01; r^2 = 0.57; AIC = 63.53; Dif. AIC = 0.00; wi = 0.84) and as a quadratic function (a1 = 18.39, b1 = 0.14, b2 = 0.00; r^2 = 0.59; AIC = 71.00; Dif. AIC = 7.47; wi = 0.02). **b)** Overall species richness (ɣ) and its development as a linear function (a1= 137.63, b1 = -0.05; r^2 = 0.74; AIC = 79.51; Dif. AIC = 0.00; wi = 0.92) and as a quadratic function (a1 = 96.47, b1 = 0.01, b2 = 0.00; r^2 = 0.74; AIC = 87.38; Dif. AIC = 7.86; wi = 0.01). **c)** Beta diversity per transect (β= γ /α) and its development as a liear function (a1 = 41.19; b1 = 0.00, r^2 = - 0.13; AIC = 21.92; Dif. AIC = 0.00; wi = 0.95) and as a quadratic function (a1 = 5.44; b1 = -0.002; b2 = 0.00; r^2 = 0.07; AIC = 29.38; Dif. AIC 7.45 ; wi = 0.02) To both approaches, linear function is more suitable to the data since for both we had lowers AIC.