ARIEL DA CRUZ REIS

TEMPERATURE AS AN IMPORTANT FACTOR DETERMINING ANT DOMINANCE

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.

Profa. Dra. Carla Rodrigues Ribas
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ARIEL DA CRUZ REIS

TEMPERATURE AS AN IMPORTANT FACTOR DETERMINING ANT DOMINANCE

TEMPERATURA COMO FATOR DETERMINANTE PARA DOMINÂNCIA EM FORMIGAS

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.

APROVADA em 28 de fevereiro de 2018.
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LAVRAS – MG
2018

FORA TEMER E TODA SUA CORJA GOLPISTA.

Dedico

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RESUMO GERAL

A dominância em formigas, ou monopolização de recursos alimentares por esses insetos, é um fato amplamente estudado na ecologia e, por vezes, considerada um fator importante para o entendimento de comunidades biológicas. No entanto, apesar de receber tal importância nas discussões em ecologia de comunidades, não existe consenso sobre o que poderia causar a ocorrência da dominância: condições, recursos, interações biológicas ou um conjunto desses fatores. Dessa forma, o objetivo central deste trabalho foi avaliar a influência da altitude sobre a dominância. Além disso, avaliamos se a temperatura, a profundidade de serapilheira e a massa seca de invertebrados da serapilheira podem influenciar a ocorrência da dominância. Para tanto, utilizamos o gradiente altitudinal do Parque Nacional do Itatiaia, já que dentro desse tipo de gradiente as variáveis avaliadas estão sujeitas a variações naturais em função da elevação. As coletas foram realizadas em sete altitudes do Parque Nacional do Itatiaia (700, 800, 1100, 1500, 1800, 2200, e 2400 m a.n.m), sempre em áreas de mata atlântica. Em cada uma das altitudes, disponibilizamos 16 iscas de sardinha e 16 iscas de mel para realizar observações da dominância. As médias anuais de temperatura foram obtidas do banco de dados do WorldClim (versão 1.4) e a profundidade de serapilheira e os invertebrados da mesma foram coletados no mesmo local onde foram disponibilizadas as iscas. A ocorrência da dominância diminuiu com o aumento da altitude, mas tal resposta não teve relação com o tipo de isca ofertada. Apesar de a temperatura ter respondido negativamente a variação da altitude, a profundidade de serapilheira e massa seca de invertebrados não mostraram relação com a altitude. Por fim, a temperatura se relacionou positivamente com a ocorrência da dominância. Nosso trabalho foi um dos poucos que mostrou como a dominância em formigas se relaciona com a variação da altitude. Além disso, mostramos que a temperatura, uma condição, foi a única variável dentre as testadas, relacionada com a resposta da dominância. Este é um importante passo para o entendimento de quais fatores determinam a ocorrência da dominância e de como ela pode ou não estar relacionada a aspectos da ecologia de comunidades.

Palavras-chave: Altitude. Monopolização de recursos. “Condições ambientais”.

ABSTRACT

Ant dominance, or the monopolization of food resources by these insects, is widely studied among ecologists and, sometimes, considered as an important factor for the understanding of biological communities. However, even though ant dominance receives a great importance in community ecology discussions, there is no consensus about what could cause its occurrence: conditions, resources, biological interactions, or a combination of these. Therefore, the aim of this work was to evaluate the influence of elevation in ant dominance. Moreover, we evaluated if temperature, leaf litter depth, and dry mass of ground dwelling invertebrates can influence the occurrence of ant dominance. To verify this, we collected our data at the elevational gradient of Parque Nacional do Itatiaia, as the variables we tested are subject to the variation of elevation. The samples were collected at seven elevations (700, 800, 1100, 1500, 1800, 2200, and 2400 m a.n.m), always in forest habitats, and for each of them we baited sardine and honey to ants. The mean annual temperature for each elevation was obtained from WorldClim dataset (version 1.4), and leaf litter depth and ground dwelling invertebrates were collect at the same points where baits were offered. The occurrence of ant dominance decreased with the increase of elevation, but this response was not related to the bait type. Only temperature had a relationship with the elevational gradient, which was negative. However, neither leaf litter depth, or dry mass of invertebrates were related to elevaiton. Finally, temperature was positively related to the occurrence of dominance. This work showed how ant dominance responds to an extensive elevational gradient. Besides, we showed that temperature, a condition, was the only variable among the tested ones that was related to ant dominance. This is an important step to the understanding of ant dominance, and how would dominance be related to aspects of community ecology.

Key words: Elevation. Resource monopolization. Environmental conditions.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

A dominância em formigas foi explorada durante muitos anos por ecólogos como um fator crucial para definir como se organizam as comunidades biológicas (Savolainen & Vepsalainen 2016; Parr 2008; Ennis & Philpott 2017). Porém, os resultados acumulados sobre o assunto ainda não trouxeram consenso entre pesquisadores sobre a real influência da dominância sobre a organização das comunidades biológicas e ainda menos consenso sobre a própria natureza da dominância em formigas, ou seja, o que levaria as espécies de formigas a exercerem dominância sobre um recurso (Ribas & Schoereder 2002; Cerdá et al. 2013; Stuble et al. 2017). Em muitos estudos, a dominância é tratada com um caso de competição por interferência, mas poucos desses estudos de fato foram capazes de testar as consequências da dominância sobre as escalas de populações e comunidades (mas veja Baccaro 2012). Se a dominância é ou não um sintoma de competição, não modifica o fato de que espécies de formigas monopolizam recursos quando esses são encontrados, impedindo o acesso de outras espécies através de comportamentos agressivos ou do recrutamento de vários indivíduos para uso do recurso (Adams 2016). Dessa forma, devemos pensar na possibilidade de a dominância não ser exclusivamente associada à competição, mas também por outros fatores como variáveis do próprio ambiente que podem indicar uma ligação da ocorrência da dominância com o contexto no qual a assembleia de formigas está inserida (Stuble et al. 2017).

Se pensarmos em formas de testar a influência de variáveis ambientais sobre comunidades biológicas, a utilização de gradientes naturais como os gradientes de altitude se mostra como uma alternativa bastante eficiente. O aumento da altitude implica em variação de condições e recursos como, por exemplo, variação de temperatura e biomassa vegetal e animal. Muitos estudos apresentam uma extensa discussão sobre a relação entre altitude e riqueza de espécies, o que nos dá um bom entendimento dos padrões de distribuição das espécies em ambientes montanos. Por exemplo, sabemos que em geral a riqueza de espécies diminui com o aumento da altitude e que essa diminuição em riqueza de espécies pode se dar de forma linear ou com um pico de riqueza em altitudes intermediárias. No entanto, essa discussão não se estende para interações entre as espécies de formigas, o que inclui a dominância. São raros os trabalhos que avaliam a relação da altitude com a dominância (mas veja

Kwon, 2016) e aqueles que o fizeram não coletaram variáveis ambientais para ajudar a explicar tal relação.

Assim, neste trabalho abordamos a dominância em formigas como um fenômeno dependente de condições e recursos. Escolhemos a temperatura como condição a ser testada como determinante para dominância e a profundidade da serapilheira e a massa seca dos invertebrados da mesma como recursos que poderiam afetar a ocorrência da dominância. A temperatura é uma condição capaz de afetar a atividade de forrageio dos animais (Pattinson and Smit 2017). Isso é ainda mais significativo para os animais ectotérmicos, uma vez que eles não podem adequar suas fisiologias de acordo com a temperatura do ambiente e compensam essa incapacidade modificando seus comportamentos (Abram et al. 2017). Ao mesmo tempo, as características do micro-habitat, tais como profundidade de serapilheira, podem influenciar a atividade de forrageio das formigas. Isso se dá pela variação da complexidade do micro-habitat, que pode influenciar a própria locomoção das formigas no ambiente (Hickey, Hollander, and Peacock 2016). Por fim, a disponibilidade de artrópodes na serapilheira poderia também influenciar a ocorrência da dominância, já que tais animais podem representar uma fonte alimentar proteica para as formigas que forrageiam na superfície do solo.

Portanto, o objetivo geral deste trabalho foi verificar se condição e recursos que variam ao longo de um gradiente altitudinal podem influenciar a ocorrência da dominância em formigas.

REFERÊNCIAS

ABRAM, P. K.; BOIVIN, G.; MOIROUX, J.; BRODEUR, J. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. **Biological Reviews**, 92, p. 1859-1876, 2017.

ADAMS, E. S. Territoriality in ants (Hymenoptera : Formicidae): a review. **Myrmicological News**, 23, p. 101-118, 2016.

BACCARO, F. B.; DE SOUZA, J. L. P.; FRANKLIN, E.; LANDEIRO, V. L.; MAGNUSSON, W. E. Limited effects of dominant ants on assemblage species richness in three Amazon forests. **Ecological Entomology**, 37, p. 1-12, 2012.

CERDÁ, X.; ARNAN, X.; RETANA, J. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? **Myrmicological News**, 18, p. 131-147, 2013.

ENNIS, K. K.; PHILPOTT, S. M. Strong influences of a dominant, ground-nesting ant on recruitment, and establishment of ant colonies and communities. Biotropica, 29, p. 521-530, 2017.

HICKEY, A.; HOLLANDER, J.; PEACOCK, M. Assessing Microhabitat Cover and Distance Effects on Harvester Ant Intraspecific Seed Preference. **Journal of Insect Behaviour**, 29, p. 535-547, 2016.

KWON, T. Foraging activity of competing ants along altitudinal gradient on a high mountain, South Korea. **Journal of Asia-Pacific Entomology**, 19, p. 95-101, 2016.

PARR, C. Dominant ants can control assemblage species richness in a South African savanna. **Journal of Animal Ecology**, 77, p. 1191-1198, 2008.

PATTINSON, N. B.; SMIT, B. Seasonal behavioral responses of an arid-zone passerine in a hot environment. **Phisiology And Behaviour**, 179, p. 268-275, 2017.

RIBAS, C. R.; SCHOEREDER, J. H. Are all ant mosaics caused by competition? **Oecologia**, 131, p. 606-611, 2002.

SAVOLAINEN, R.; VEPSÄLÄINEN, K. A Competition Hierarchy among Boreal Ants: Impact on Resource Partitioning and Community Structure. **Oikos**, 51, p. 135, 1988.

STUBLE, K. L.; JURIĆ, I.; CERDÁ, X.; SANDERS, N. J. Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? and what is a dominance hierarchy anyways? **Myrmicological News**, 24, p. 71-81, 2017.

SEGUNDA PARTE

ARTIGO

Versão preliminar para Journal of Biogeography

Artigo - The Hotter the Feistier! Temperature as an Important Factor to Determine Ant Dominance

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ABSTRACT

Aim: The main objective of this work was to test the influence of elevation on ant dominance. Moreover, we tested if temperature, leaf litter depth, and dry mass of ground dwelling invertebrates would vary along elevation, and if these factors would influence ant dominance.

Location: Parque Nacional do Itatiaia, southeastern Brazil.

Methods: Ant dominance was observed and quantified using honey and sardine baits. The observations occurred troughout an elevational gradient ranging from 700 to 2045 m a.s.l. A squared meter of leaf litter was sampled at each point to measure leaf litter depth, and to collect ground dwelling invertebrates. Temperature was obtained from the WorldClim (version 1.4) dataset. We used generalized linear models to test the relationship between (1) dominance and elevation, (2) temperature, leaf litter depth, and dry mass of invertebrates and elevation, and (3) dominance and temperature.

Results: Ant dominance had a linear and negative relationship with elevation, and this relationship was not influenced by the bait type (honey or sardine). Only temperature responded to the elevational gradient, decreasing with the increase of elevation. Finally, temperature had a positive effect on the dominance occurrence.

Main Conclusions: This is one of the few studies that evaluated how ant dominance responds to an elevational gradient. Moreover, our work showed that temperature was more relevant to understand the occurrence of dominance than the than leaf litter depth or dry mass of invertebrates. Therefore, if ant dominance is indeed related to aspects of community ecology, we should expect that its effects to biological communities are going to be dependent on the environmental conditions besides other variables. Future studies must find an experimental design to really test the relationship between ant dominance and community parameters, such as species richness.

Keywords: Elevation. Resource monopolization. Environmental conditions.

2 INTRODUCTION

For many years ant dominance was considered a hallmark of ant ecology, but recently this idea has been questioned and ecologists have approached ant dominance with new perspectives (Cerdá, Arnan, and Retana 2013; Stuble et al. 2017). These perspectives take into account that many studies on ant dominance do not define what exactly a dominance hierarchy is, and do not evaluate what may be triggering dominance to occur. Therefore, we must analyze dominance thoroughly, with clear concepts, and fully understand what may influence the occurrence of dominance.

There are three main approaches for ant dominance among ecological studies: numerical, specifically referring to the relative abundance of a given species at an area or at a bait; behavioral, which is related to interactions among species that culminate in one species monopolizing food resources; and ecological, understood as a combination of both numerical and behavioral dominance, (Cerdá, Arnan, and Retana 2013).

Temperature is an example of an important factor that can determine animal activity, including foraging behaviors (Pattinson and Smit 2017). In the case of ectotherms, such as insects, coping with temperature can be translated into behavioral adjustments, as they cannot adjust their body temperature by physiological changes (Abram et al. 2017). Temperature can influence ant foraging period and intensity, or even its aggressiveness (Castro et al. 2017; Segev et al. 2017). Considering these effects of temperature in ant activity, it is plausible that dominance can also be affected by this condition. Another factor that may influence the occurrence of dominance is the physical structure of the microhabitat. For ground dwelling ants, leaf litter characteristics can influence ant activity either by increasing the locomotion difficulties (Hickey, Hollander, and Peacock 2016), or by changing the abundance of food resources on the ground (Parui, Chatterjee, and Basu 2015). The amount of leaf litter can increase the number of other invertebrates on the ground, consequently increasing the amount of protein resources for ants.

An efficient way to test the influence of environmental variables is to use natural gradients, such as elevational gradients. The increase on elevation implies in variation of conditions and resources, for example, temperature, and biomass (Körner

2007). Moreover, sampling along mountains facilitate the data collection, as natural variation occurs in a small geographical space if compared, for example, to latitudinal gradients.

Considering physical conditions varying along an elevational gradient and dominance related to ant activity and foraging behavior, we aimed to understand how ant dominance varies with an elevational gradient. Our first goal was to find the general relationship between dominance and elevation, and we hypothesized that dominance would decrease at higher elevations. Our second goal was to split elevation into temperature, leaf litter depth, and dry weight of ground dwelling invertebrates, to examine their variation with altitude. Finally, our last goal was to test which combination these environmental factors could influence dominance. Our results showed that elevation negatively influence dominance, and that temperature is explaining this relationship.

3 MATERIALS AND METHODS

3.1 Study Area

Field work was carried out at the Parque Nacional do Itatiaia (PNI hereafter). Located at Brazilian southeastern region (22º16’ - 22º28’ S and 44º34’ - 44º42’ W), PNI is classified into two categories of the Köppen climate classification: CWB (mesothermic, with a mild summer and a dry winter) and CPB (mesothermic, mild summer, without a defined dry season). Data sampling was done during the ending of wet season. The mean annual temperature registered at the highest point of the park is 11.5ºC; however, considering the great variation due to elevation, the overall mean for minimum and maximum temperature is 15ºC and 18ºC, respectively. Finally, the most representative vegetation is Atlantic Forest, particularly ombrophilous dense forest (Brasília, 2016), and all samples came from this type of vegetation.

3.2 Data Sampling

To test the relationship between ant dominance and the elevational gradient, we sampled ants at seven elevations in the Parque Nacional do Itatiaia. Each elevation was separated geographically from each other by at least 1 km, representing the following altitudes: 700, 800, 1100, 1500, 1800, 2200, and 2400 m a.s.l. For each altitude we set up 16 sampling points. At each sampling point we baited 4 g of sardine and a soaked cotton ball with 4 mL of a honey solution to ants, using a plastic surface to dispose each type of bait.

Ant dominance was observed at each bait, which was checked six times for 2 min, totalizing 12 min of observations per bait. The observations always started at 2 pm. Dominance was characterized according to the suggestion of Doctor Ricardo Campos (personal communication, 2016). We considered the occurrence of dominance when an ant species found a bait, expelled other species from it, and increased in number overtime. Any ant present at the end of the observation period was collected, identified, and submitted to the reference collection at Laboratório de Ecologia de Formigas of the Universidade Federal de Lavras.

To test the variation of conditions and resources throughout the elevational gradient we also sampled leaf litter depth and dry weight of ground dwelling invertebrates after the ant observations were over. Leaf litter depth was related to the microhabitat structure, and the weight of invertebrates to the availability of food resources. To measure the leaf litter depth, we used a PVC quadrate to define 1 m^2 area around the baits and measured the leaf litter with a ruler at two vertexes of the quadrate, as well as its center. The final leaf litter depth was the mean of the three measurements.

To calculate the invertebrates' biomass, we used the same quadrate area, and sampled leaf litter to extract invertebrates with the Winkler extractor method (ALL Protocol). Winkler extractors were set up for 72 h, and all collected invertebrates were preserved in alcohol (70%). At the laboratory, we sorted the samples separating ants and other invertebrates. The invertebrates were dried at 40° C, and weighted.

Temperature was obtained from the database of the WorldClim (1.4 version). We used the data of mean annual temperature for each elevation. The geographical separation of at least 1 Km between each elevation guaranteed that temperature data were independent for each point, as the pixels of satellite images from WorldClim are scaled for 1 Km.

3.3 Statistical Analyses

To test the relationship between ant dominance and the elevational gradient we first built a generalized linear model (GLM) including the type of bait in the model to examine the influence of bait on dominance. We used the frequency of dominated baits as our dependent variable and tested the influence of elevation, type of bait, and the interaction between these two. We then simplified the model removing the variables that were not significant to the relationship between dominance and the elevational gradient.

To examine the variation of conditions and resources with the elevational gradient, we performed GLM's, considering as dependent variables the mean leaf litter depth, mean biomass of invertebrates, and mean temperature and elevation as the independent variable.

Finally, to test the relationship amongst ant dominance, temperature, leaf litter depth, and biomass of invertebrates we also used a GLM. For this model, ant dominance was our dependent variable, whereas our independent variables were the ones that varied with elevation. All analyses were performed with R software (R core team, 2016)

4 RESULTS

We observed a total of 52 ant species at baits (Table 1). The most representative subfamily was Mirmycinae with 41 species, being 31 of them from the genus *Pheidole*. *Megalomyrmex* was the only genus found at the five first consecutive elevations. Interestingly, the two species of *Megalomyrmex* occurred separated in the elevational gradient, coinciding only at the elevation of 1100 m.

Dominance was not influenced by bait type ($F = 2.51$, $p = 0.1$, $df = 12$; Figure 1 a) or the interaction between bait and elevation ($F= 1.32$, $p = 0.2$). Therefore, we summed the number of dominated sardine and honey baits, and found that dominance responds negatively to the increase of elevation ($F = 41.24$, $p = 0.001$; Fig. 1 b). The number of dominated baits dropped with the increase of elevation until it gets to zero at the two highest altitudes (2.200 and 2.400 m a.s.l.). Interestingly, the number of species observed at baits was also lower for these two elevations.

When we tested the variation of conditions and resources throughout the elevational gradient, we found that only temperature responded to elevation, decreasing as elevation increased ($F = 157.79$, $p < 0.001$; Figure 2a). Both leaf litter depth and dry mass of invertebrates did not vary in response to the elevational gradient ($F = 5.38$, $p = 0.06$; Figure 2b, and $F = 0.04$, $p = 0.8$; Figure 2c, respectively).

Finally, we found that the only variable influencing ant dominance was temperature ($F = 25$, $p < 0.01$; Fig 3). Temperature alone had the opposite effect on ant dominance that elevation had. The increase of temperature was followed by an increase in ant dominance.

5 DISCUSSION

We corroborated our hypothesis that dominance would decrease with the increase of elevation, showing a linear and negative effect of elevation on ant dominance. Moreover, we could show that dominance had the same response throughout elevations independently of the bait type (protein and carbohydrate sources).

As we showed that dominance varies with elevation, we had an indication that some ecosystem properties may be also varying with this gradient, and influencing the occurrence of dominance. This relationship between environmental changes related to elevation and their effects on biological communities is better understood for plants (Mayor et al., 2017). However, our results indicate that this relationship may also be true for animals. Nevertheless, the occurrence of dominance was not related to the bait type, dominance decreased at higher elevations independently of the food resource that was offered. That was contrary to our expectations as ant behaviors, such as aggressiveness, can be influenced by the availability of macronutrients such as

proteins and carbohydrates (Grangier & Lester, 2014). Therefore, it seems that these nutrients are not scarce or varying at the system we have studied.

It is rare to find a study that shows how ant dominance vary with elevation (but see Spotti et al. 2015 and Kwon 2016), but our study gave us a glimpse of this general pattern, bringing us to our second aim that was to divide elevation into more explanatory variables and see what may explain the variation of dominance.

We found that only the variation of temperature was influenced by elevation, but leaf litter depth, or biomass of invertebrates were not. The response of temperature to elevation has been long documented (Körner 2007, Sundqvist et al. 2013) and coherent among studies: the increase of elevation causes a decrease of temperature. As for the other variables, we expected that leaf litter depth would be greater at higher elevations and the dry weight of invertebrates would decrease at higher elevations. The low temperatures at high elevations can inhibit the action of microorganisms, and slow down the decomposition of leaf litter (Marian et al. 2017; Liu et al. 2017). However, in our study the depth of accumulated leaf litter did not respond exactly that way, even though we observed a tendency of greater leaf litter depth at higher elevations (Fig. 2). Taylor et al. (2017) suggest that the decomposition of leaf litter can be better explained by a combination between temperature and precipitation. As we did not measure precipitation in our study, we can only hypothesize that precipitation patterns at Parque Nacional do Itatiaia may work with temperature and create a different outcome for leaf litter decomposition. At last, for the invertebrates' biomass, we assumed that this variable would decrease at higher elevations because productivity is usually lower at mountaintop and cannot sustain a great abundance of animals. Xu et al. (2017) argue that microhabitat complexity is an important factor to explain litter dwelling invertebrates. As we did not observe a linear variation of leaf litter across elevations, the microhabitat for litter invertebrates may also have not varied and we did not observe a response for dry weight of invertebrates. Therefore, temperature was the variable that could explain the variation of ant dominance in our study.

We showed that temperature had a positive relationship with the occurrence of ant dominance (Fig. 3). Temperature is well known to constraint insect activity (Abram et al. 2017) and that can be extended to ant dominance. There has been a long discussion about how temperature can mediate the occurrence of dominance (Cerdá, Arnan, and

Retana 2013; Kaspari et al. 2015; Spicer et al. 2017). The most common of them is the thermal tolerance trade-off, which postulates that dominant and non-dominant ant species have different ranges of thermal tolerances, and avoid each other by foraging under different temperatures (Cerdá, Retana, and Manzaneda 1998). This discussion has been made based in studies carried out comparing different habitats (Lessard, Dunn, and Sanders 2009; Wittman et al. 2010; Stuble et al. 2013), but our study show that ant dominance is controlled by temperature even at the same ecosystem. This is important because we take out the assumption that the result is context-dependent, i.e., the assemblage we sampled had the same evolutionary history, and is under the same variation of conditions (in this case, temperature). This explanation is plausible to our work, since most species found at lower elevations are not found at highest ones, where dominance was not recorded (Table 1). Though the thermal tolerance trade-off can be evoked to explain our results, we can also suggest that temperature may simply decrease the chances that two species would encounter each other in the field, and that would decrease the occurrence of dominance. That can happen as temperature is also related to the number of species at local scale, abundance, and ant activity (McCain, 2007; Segev et al., 2017). Summing all these outcomes controlled by temperature, we have an environment where the chances for two ant species to encounter would be very low. To test that, we suggest that new studies evaluate if the ant assemblage at a given place is coincident with the assemblage occurring at baits. That would indicate if ant species are avoiding each other, or just are not occurring at the same patch.

6 CONCLUSIONS

Our study showed a general pattern of ant dominance throughout an elevational gradient: ant dominance decreases as a response to elevation increase. This is a new approach to ant dominance and may be a new step to the understanding of this ant behavior, since our results show that temperature in the elevational gradient is capable of influencing the occurrence of dominance. This study showed that temperature is more important to explain ant dominance than leaf litter depth and biomass of invertebrates. In this case, our results may contribute to the current discussion about in

what contexts dominance can be relevant to the understanding of biological communities. Now, future studies should focus on other variables that could also influence dominance occurrence and to test if ant dominance is able to affect the cooccurrence of species.

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REFERENCES

Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biological Reviews, 92(4), 1859-1876.

Agosti, D., & Alonso, L. E. (2000). The ALL protocol. Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, 280, 204-206.

Castro, G. H., Kayano, D. Y., Souza, R. F., Hilsdorf, A. W., Feitosa, R. M., & Morini, M. S. (2017). Seasonal Patterns of the Foraging Ecology of Myrmelachista arthuri Forel, 1903 (Formicidae: Formicinae). Sociobiology, 64(3), 237-243.

Cerdá, X., Retana, J., & Manzaneda, A. (1998). The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia, 117(3), 404-412.

Cerda, X., Arnan, X., & Retana, J. (2013). Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. Myrmecological News, 18, 131-147.

Grangier, J., & Lester, P. J. (2014). Carbohydrate scarcity increases foraging activities and aggressiveness in the ant Prolasius advenus (Hymenoptera: Formicidae). Ecological entomology, 39(6), 684-692.

Hickey, A., Hollander, J., & Peacock, M. (2016). Assessing Microhabitat Cover and Distance Effects on Harvester Ant Intraspecific Seed Preference. Journal of insect behavior, 29(5), 535-547.

Kaspari, M., Clay, N. A., Lucas, J., Yanoviak, S. P., & Kay, A. (2015). Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Global change biology, 21(3), 1092-1102.

Körner, C. (2007). The use of 'altitude' in ecological research. Trends in ecology & evolution, 22(11), 569-574.

Kwon, T. S. (2016). Foraging activity of competing ants along altitudinal gradient on a high mountain, South Korea. Journal of Asia-Pacific Entomology, 19(1), 95-101.

Lessard, J. P., Dunn, R. R., & Sanders, N. J. (2009). Temperature-mediated coexistence in temperate forest ant communities. Insectes Sociaux, 56(2), 149-156.

Liu, G., Sun, J., Tian, K., Yuan, X., An, S., & Wang, H. (2017). Litter decomposition of emergent plants along an elevation gradient in wetlands of Yunnan Plateau, China. Chinese Geographical Science, 27(5), 760-771.

Marian, F., Sandmann, D., Krashevska, V., Maraun, M., & Scheu, S. (2017). Leaf and root litter decomposition is discontinued at high altitude tropical montane rainforests contributing to carbon sequestration. Ecology and evolution, 7(16), 6432-6443.

Mayor, J. R., Sanders, N. J., Classen, A. T., Bardgett, R. D., Clément, J. C., Fajardo, A., ... & Cieraad, E. (2017). Elevation alters ecosystem properties across temperate treelines globally. Nature, 542(7639), 91.

McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and biogeography, 16(1), 1-13.

Parui, A. K., Chatterjee, S., & Basu, P. (2015). Habitat characteristics shaping ant species assemblages in a mixed deciduous forest in Eastern India. Journal of Tropical Ecology, 31(3), 267-280.

Pattinson, N. B., & Smit, B. (2017). Seasonal behavioral responses of an arid-zone passerine in a hot environment. Physiology & behavior, 179, 268-275.

Segev, U., Burkert, L., Feldmeyer, B., & Foitzik, S. (2017). Pace-of-life in a social insect: behavioral syndromes in ants shift along a climatic gradient. Behavioral Ecology, 28(4), 1149-1159.

Spicer, M. E., Stark, A. Y., Adams, B. J., Kneale, R., Kaspari, M., & Yanoviak, S. P. (2017). Thermal constraints on foraging of tropical canopy ants. Oecologia, 183(4), 1007-1017.

Spotti, F. A., Castracani, C., Grasso, D. A., & Mori, A. (2015). Daily activity patterns and food preferences in an alpine ant community. Ethology Ecology & Evolution, 27(3), 306-324.

Stuble, K. L., Rodriguez-Cabal, M. A., McCormick, G. L., Jurić, I., Dunn, R. R., & Sanders, N. J. (2013). Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities. Oecologia, 171(4), 981-992.

Stuble, K. L., Jurić, I., Cerda, X., & Sanders, N. (2017). Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? And what is a dominance hierarchy anyways? Myrmecological News, 24, 71-81.

Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annual Review of Ecology, Evolution, and Systematics, 44, 261-280.

Taylor, P. G., Cleveland, C. C., Wieder, W. R., Sullivan, B. W., Doughty, C. E., Dobrowski, S. Z., & Townsend, A. R. (2017). Temperature and rainfall interact to control carbon cycling in tropical forests. Ecology letters, 20(6), 779-788.

Wittman, S. E., & Gotelli, N. J. (2011). Predicting community structure of ground-foraging ant assemblages with Markov models of behavioral dominance. Oecologia, 166(1), 207-219.

Xu, G., Lin, Y., Zhang, S., Zhang, Y., Li, G., & Ma, K. (2017). Shifting mechanisms of elevational diversity and biomass patterns in soil invertebrates at treeline. Soil Biology and Biochemistry, 113, 80-88.

Figure 1 – Response of ant dominance to elevation. Dominance is represented as the total number of dominated baits at each elevation. a) Influence of elevation in ant dominance separated by the bait type. Bait type did not influence the occurrence of dominance ($F = 2.43$, $p = 0.14$, $n = 32$). b) Influence of elevation in ant dominance regardless of the bai type. Elevation had a significant influence on dominance occurrence ($F = 41.24$, $p < 0.01$, $n = 16$). The shaded area shows the 95% confidence interval of the relationship between dominance and elevation.

Figure 2 - Response of condition (temperature) and resources (litter depth and weight of invertebrates) to elevation. All dependent variables are mean values at each elevation, and temperature is an annual mean. a) Response of temperature to elevation. The temperature was the only variable among the ones we tested that responded to elevation ($F = 157.79$, $p < 0.001$, $n = 7$). b) Response of litter leaf depth to elevation. The leaf litter depth variation did not show influences of elevation ($F= 5.38$, $p = 0.06$, $n = 7$). c) Response of the dry mass of invertebrates to elevation. The dry mass of invertebrates was also not influenced by elevation ($F= 0.043$, $p = 0.8$, $n = 7$).

Figure 3 - Influence of temperature in ant dominance. Dominance is represented as the total number of dominated baits at each elevation, and temperature is the annual mean temperature. Dominance occurrence showed a strong and positive relationship to elevation ($F= 25.17$, $p < 0.01$, n 16). The shaded area represents the 95% interval of confidence of the relationship between dominance and temperature.

Table 1 - Species occurrence at each elevation of Parque Nacional do Itatiaia. The “x” in the table indicates the occurrence of the species at a sardine bait, honey bait, or both. Last line shows the total number of species at each elevation.

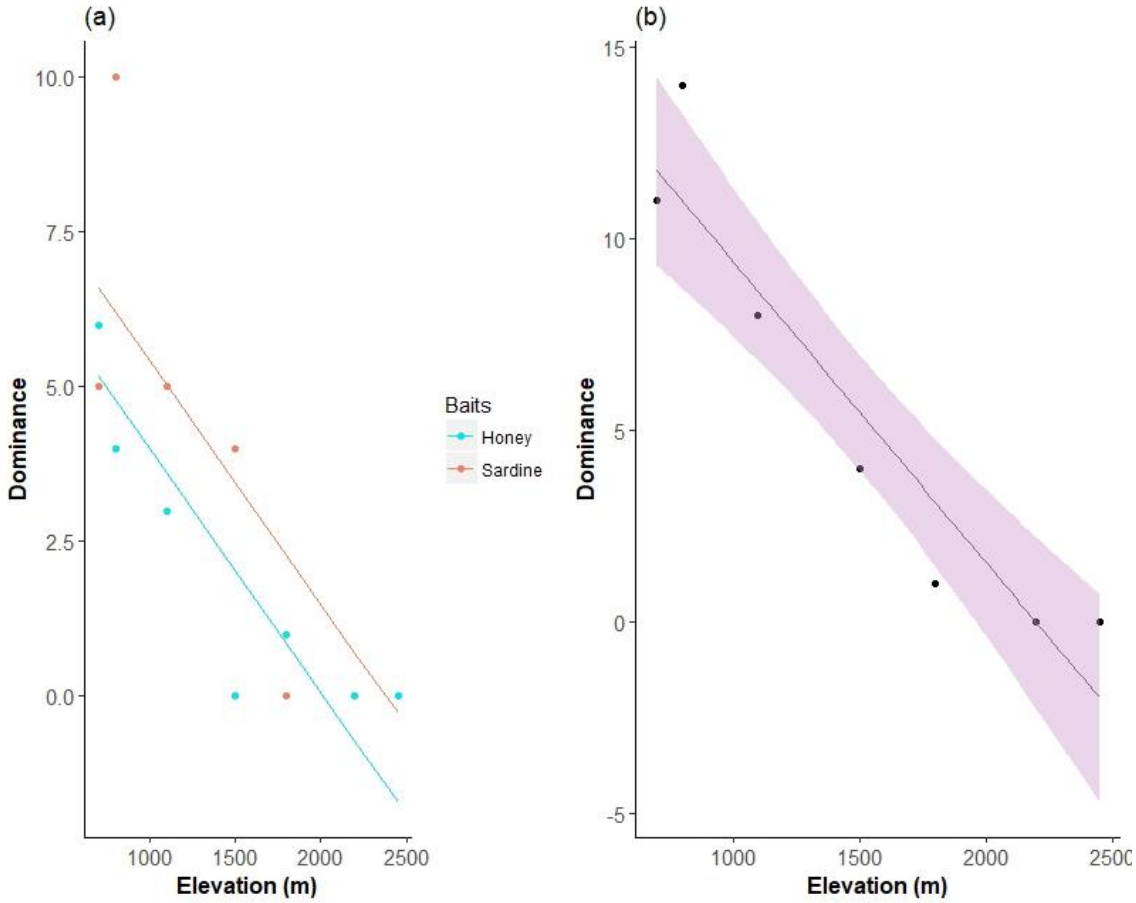
(a)
10.0
7.5
5.0
2.5
0.0
Dominance
1000
1500
2000
2500
Elevation (m)
Baits
Honey
Sardine
(b)
15
10
5
0
-5
Dominance
1000
1500
2000
2500
Elevation (m)

Figure 1

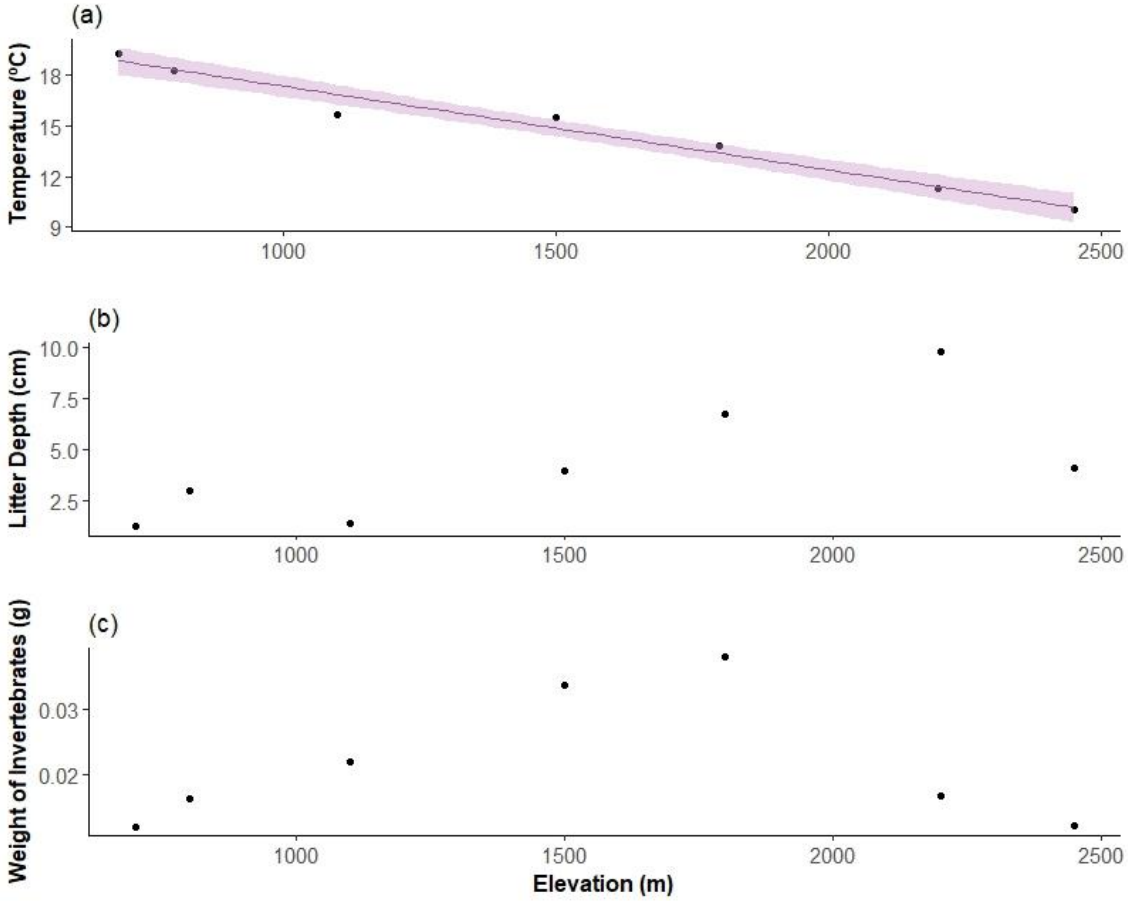
(a)
Temperature (°C)
18
15
12
9
1000
1500
2000
2500
(b)
Litter Depth (cm)
10.0
7.5
5.0
2.5
1000
1500
2000
2500
(c)
Weight of Invertebrates (g)
0.03
0.02
1000
1500
2000
2500
Elevation (m)

Figure 2

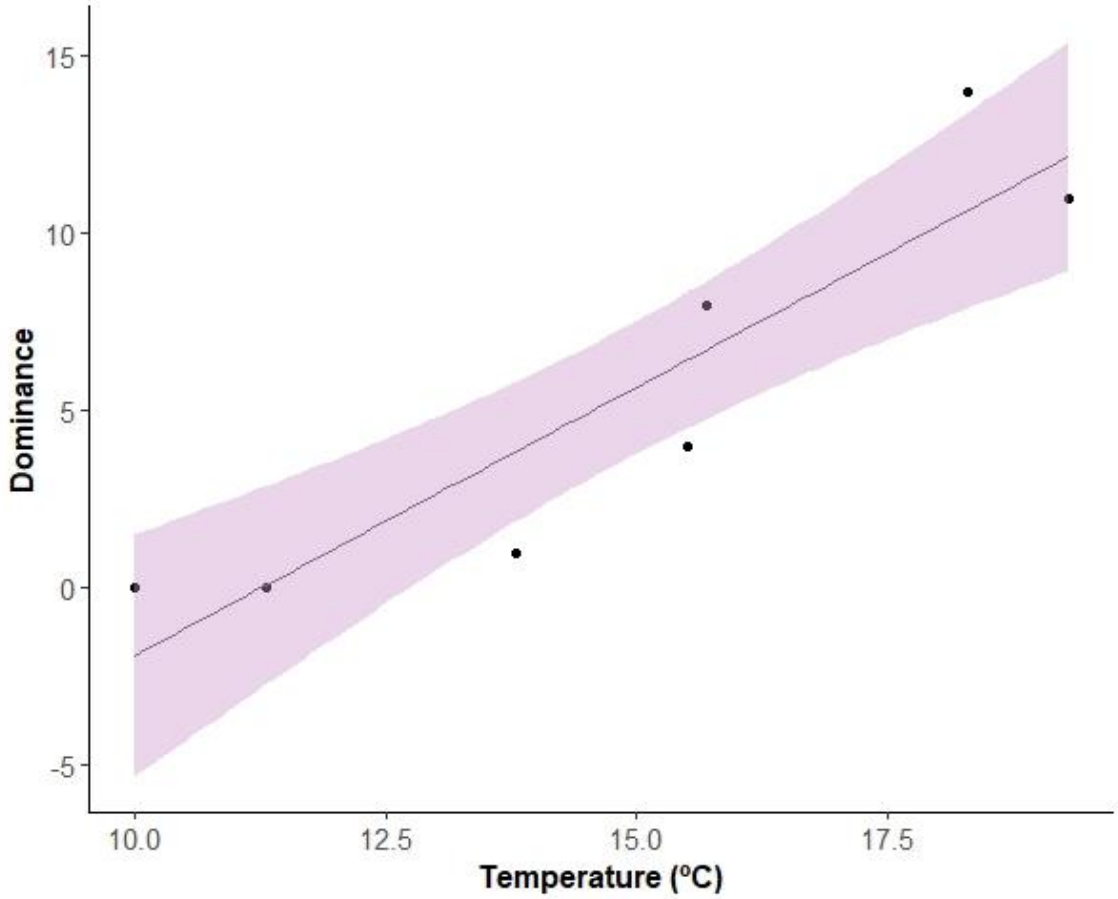

Figure 3

Table 1

Elevation (m a.s.l.)	700	800	1100	1500	1800	2200	2450
Camponotus rufipes			x			x	
Pachycondyla striata	x	x	x				
***Wasmannia* sp1**					x	x	x
***Wasmannia* sp2**		x		x	x		
Gnamptogenys striatula			x				
Ectatomma edentatum		x					
***Nylanderia* sp6**			x				
Oxyepoecus reticulatus					x		
***Brachymyrmex* sp1**				x			
***Brachymyrmex* sp2**							x
***Solenopsis* sp1**	x	x	x				
***Solenopsis* sp2**	x	x	x				
***Crematogaster* sp1**		x					
***Crematogaster* sp2**	x						
***Crematogaster* sp3**	x	x					
***Crematogaster* sp4**	x						
Megalomyrmex goeldii	x	x	x				
Megalomyrmex pusillus			x	x	x		
***Pheidole* sp1**		x					
***Pheidole* sp2**	x	x		x			
***Pheidole* sp3**	x						
***Pheidole* sp4**				x			
***Pheidole* sp5**	x						
***Pheidole* sp6**			x	x			
***Pheidole* sp7**		x					
***Pheidole* sp8**			x				
Pheidole mosenopsis	x						
***Pheidole* sp9**				x			
***Pheidole* sp10**	x	x					
***Pheidole* sp11**						x	
***Pheidole* sp12**	x						
***Pheidole* sp13**			x	x			
Pheidole ambigua				x			
***Pheidole* sp14**					x		

***Pheidole* sp15**				x			
Pheidole senilis			x	x			
Pheidole guilelminuelleri	x						
Pheidole aff. sigillata	x						
Pheidole germaini		x					
***Pheidole* sp16**		x					
***Pheidole* sp17**		x					
***Pheidole* sp18**					x	x	x
***Pheidole* sp19**						x	x
Pheidole gertrudae	x						
***Pheidole* sp20**		x					
***Pheidole* sp21**				x			
Pheidole tristis			x				
***Pheidole* sp22**		x					
Pheidole sarcina				x			
***Linepithema* sp1**	x		x				
***Linepithema* sp2**			x	x			
***Linepithema* sp3**		x	x				
Total Number of Species	17	18	15	14	6	5	4

CONSIDERAÇÕES FINAIS

Mostramos em nosso trabalho que a altitude de fato influencia a ocorrência da dominância em formigas. A dominância mostrou uma relação linear negativa com a altitude. Mais do que isso, pudemos verificar que a condição temperatura teve uma relação linear positiva com a dominância, mas profundidade de serapilheira e massa seca de invertebrados não apresentaram relação com a dominância. Entender que uma condição do ambiente apresenta mais influência sobre a dominância do que os recursos nos indica que a dominância de fato deve ser explorada por mais pontos de vista além da competição.

Além disso, tais resultados nos estimulam a pensar em outras possíveis variáveis, possivelmente condições, que possam influenciar a dominância em formigas. Por fim, cientistas deveriam começar a buscar novos desenhos amostrais que de fato demonstrem que a dominância em formigas seja capaz de influenciar parâmetros das assembleias de formigas como por exemplo a riqueza de espécies. Dessa forma, poderíamos demonstrar que a baixa co-ocorrência das espécies de formigas pode ser determinada por condições como a temperatura, e não por competição como geralmente é colocado por cientistas.