Instituto Nacional de Pesquisas da Amazônia – INPA

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EVOLUÇÃO DEBAIXO DO NOSSO NARIZ: DIVERGÊNCIA ECOLÓGICA ENTRE POPULAÇÕES SIMPÁTRICAS DE UM ARTRÓPODE EDÁFICO

Pedro Aurélio Costa Lima Pequeno

Manaus, Amazonas

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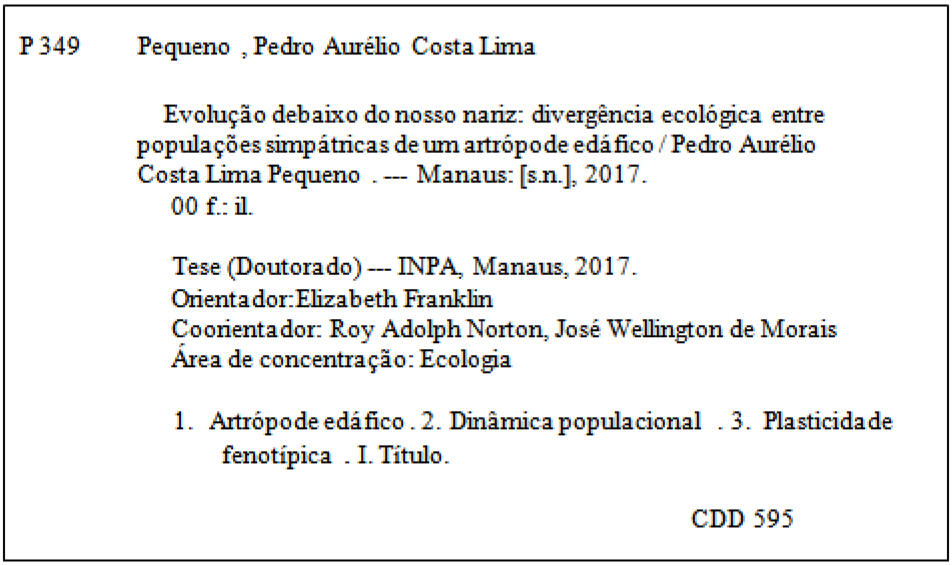

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Sinopse:

Estudou-se o papel da heterogeneidade topográfica na divergência ecológica entre populações simpátricas de artrópodes edáficos. Para isto, usou-se como modelo o ácaro partenogenético *Rostrozetes ovulum* (Berlese, 1908), dos quais foram coletados dados referentes à distribuição espaço-temporal, morfologia e fisiologia em um fragmento florestal urbano (800 ha) na Amazônia central.

Palavras-chave: Adaptação, dinâmica populacional, evolução, especiação, história de vida, plasticidade fenotípica

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“*Ecologia é a ciência das relações do organismo com o ambiente circundante, o qual inclui, em sentindo amplo, todas as condições para sua existência. Estas condições podem ser orgânicas ou inorgânicas; ambas são da maior importância para a forma dos organismos, porque elas forçam o organismo a se adaptar*.” (Ernst Haeckel, 1866)

RESUMO

A origem de novas espécies, ou especiação, é comumente descrita como evolução de incompatibilidades reprodutivas. Curiosamente, muitos organismos especiaram na ausência de reprodução sexuada, sugerindo que a diversificação da vida pode depender mais de oportunidades à adaptação que de barreiras à reprodução cruzada. Entretanto, pouco se sabe sobre quais fatores ambientais atuam como agentes seletivos, e em quais circunstâncias. Esta tese investigou estas questões usando um artrópode edáfico cosmopolita, o ácaro partenogenético *Rostrozetes ovulum* (Berlese, 1908). Testou-se a hipótese de que o mosaico topográfico típico das florestas de terra firme da Amazônia promove divergência adaptativa entre populações simpátricas em função do risco de alagamento. Para isto, populações de *R. ovulum* distribuídas entre platôs e baixios foram estudadas em um fragmento florestal urbano (800 ha). No capítulo 1, mostra-se que o padrão espacial de distribuição de *R. ovulum* muda sazonalmente, salientando a importância da consideração simultânea de espaço e tempo em estudos ecológicos. No capítulo 2, revela-se que, independentemente do hábitat, a densidade populacional aumenta com o tamanho corporal médio dos adultos (uma medida do potencial reprodutivo), ao mesmo tempo em que diminui com a força da denso-dependência (uma medida do grau de competição intraespecífica), revelando o papel simultâneo do fenótipo e do ambiente na dinâmica populacional. No capítulo 3, mostra-se que o grau de plasticidade sazonal do tamanho corporal é maior nos baixios que nos platôs, consistente com ideias recentes sobre o papel adaptativo da plasticidade fenotípica perante limitação de oxigênio (i.e. solos alagáveis). No capítulo 4, revela-se o papel seletivo do risco de alagamento através de dados morfofisiológicos de *R. ovulum*: nos baixios, os indivíduos tendem a conter mais rugosidades cuticulares e, em menor grau, a serem mais ovais e menores que nos platôs, ao mesmo tempo em que conseguem sobreviver por mais tempo à submersão. Demonstra-se também que a divergência morfofisiológica entre hábitats é independente da distância geográfica entre populações, a qual não tem qualquer efeito sobre a diferenciação fenotípica observada. Isto sugere que a dispersão não é um fator limitante no sistema estudado e, portanto, a divergência observada provavelmente é mantida por processos contemporâneos. Esta tese evidencia divergência ecológica, morfológica e fisiológica em extensões espaciais relativamente pequenas, e na ausência de reprodução sexuada. Paisagens heterogêneas podem ser importantes não só para a manutenção da grande diversidade dos solos, mas também para sua criação.

EVOLUTION UNDER OUR NOSE: ECOLOGICAL DIVERGENCE AMONG SYMPATRIC POPULATIONS OF A SOIL ARTHROPOD

ABSTRACT

The origin of new species, or speciation, is often described as the evolution of reproductive incompatibilities. Curiously, many organisms speciated while being asexual, suggesting that the diversification of life may depend more on opportunities for adaptation than on barriers to crossed reproduction. However, little is known about which environmental factors function as selective agents, and under which circumstances. This dissertation investigated these issues using a cosmopolitan soil arthropod, the parthenogenetic mite *Rostrozetes ovulum* (Berlese, 1908). The hypothesis was tested that the topographic mosaic typical of Amazonian *terra firme* forests promotes adaptive divergence among sympatric populations as a function of submersion risk. To this aim, *R. ovulum* populations distributed between uplands and valleys were studied in a urban forest remnant (800 ha). In chapter 1, it is shown that the spatial distribution pattern of *R. ovulum* changes seasonally, stressing the importance of the simultaneous consideration of space and time in ecological studies. In chapter 2, it is revealed that, independently of habitat, population density increases with mean adult body size (a measure of reproductive potential) while it decreases with the strength of density dependence (a measure of the level of intraspecific competition), stressing the simultaneous role of phenotype and environment in population dynamics. In chapter 3, it is shown that the degree of seasonal plasticity in body size is higher in valleys than in uplands, consistent with recent ideas on the adaptive role of phenotypic plasticity under oxygen limitation (i.e. hydromorphic soils). In chapter 4, the selective role of habitat submersion risk is revealed through morpho-physiological data on *R. ovulum*: in valleys, individuals tend to have more cuticular rugosities and, to a lesser degree, to be more slender and smaller than in uplands, while being able to survive submersion longer. It is also shown that the morpho-physiological divergence between habitats is independent of the geographic distance among populations, which has no effect on the observed phenotypic differentiation. This suggests that dispersal is not a limiting factor in the studied system and, thus, the observed divergence is likely maintained by contemporary processes. This dissertation evidences ecological, morphological and physiological divergence in relatively small spatial extents, and in the absence of sexual reproduction. Heterogeneous landscapes could be important not only in the maintenance of the high diversity of soils, but also in its creation.

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Síntese

Figura 1. Síntese das relações investigadas nesta tese. As caixas representam variáveis, agrupadas em três categorias: ambiente (verde), fenótipo (laranja) e dinâmica populacional (azul). Setas unidirecionais representam relações causais; setas bidirecionais representam correlações de natureza indefinida. Setas pretas indicam relações estatisticamente significativas; setas cinzas representam relações marginalmente significativas.

INTRODUÇÃO GERAL

Darwin & Wallace (1858) revolucionaram as ciências naturais ao sugerir que novas espécies surgem por divergência adaptativa perante condições ambientais contrastantes. A fim de atrair interesse para esta questão, Haeckel (1866) propôs uma nova disciplina, criando o termo "ecologia". Para Haeckel e outros evolucionistas do séc. XIX, "espécies" eram segmentos arbitrários de um contínuo de variação, e ecologia era o estudo da evolução ao longo deste contínuo. No século seguinte, porém, espécies passaram a ser vistas como populações isoladas reprodutivamente que poderiam evoluir por deriva genética pura e simples, desde que o fluxo gênico entre elas fosse limitado (Mallet 2008; Bird *et al.* 2012). Rapidamente, especiação por isolamento geográfico passou a ser vista como mais provável que especiação por adaptação, e o estudo da diversificação voltou-se à biogeografia e à filogenética (Mallet 2008; Bird *et al.* 2012; Nosil 2012). Paralelamente, ecólogos passaram a associar sua disciplina mais a padrões de distribuição e abundância que à evolução (Scheiner & Willig 2008).

Apesar disso, ecologia e diversificação têm se reaproximado em anos recentes, graças a algumas descobertas decisivas: (1) o grau de incompatibilidade reprodutiva aumenta continuamente com a distância genética entre populações, desde populações consideradas coespecíficas até populações consideradas heteroespecíficas (Mallet 2008); (2) a distância genética entre populações aumenta com a divergência ecológica entre elas, independentemente da distância geográfica (Shafer & Wolf 2013); e (3) o grau de incompatibilidade reprodutiva aumenta com a divergência ecológica entre populações, independentemente da distância genética entre elas (Funk, Nosil & Etges 2006). Tais achados revigoram a proposição original de Darwin & Wallace (1858): novas espécies podem surgir frequentemente por seleção divergente imposta pelo ambiente – hoje mais conhecida como "especiação ecológica" (Nosil 2012; Langerhans & Riesch 2013; Shafer & Wolf 2013).

A despeito da importância da seleção na diversificação biológica, a identidade dos agentes seletivos – os fatores ambientais (i.e. recursos, condições abióticas) que causam diferença de sucesso reprodutivo entre fenótipos – é desconhecida na maioria dos casos, assim como as circunstâncias que levam um fator ambiental a atuar como agente seletivo (MacColl 2011; Kingsolver *et al.* 2012). Além disso, existem pelo menos três fatores que podem dificultar a divergência adaptativa entre populações: migração, plasticidade fenotípica e reprodução sexuada. Primeiro, a migração tende a misturar alelos entre populações e, portanto, a homogeneizar suas composições genéticas, freando sua diferenciação (Futuyma

2010). Se a dispersão é um fator limitante, podemos esperar que, quanto mais próximas as populações estiverem entre si, mais parecidas elas tenderão a ser (Shafer & Wolf 2013). Segundo, a plasticidade fenotípica permite que um mesmo genótipo expresse diferentes fenótipos, dependendo das condições ambientais. Quando a plasticidade se manifesta durante a fase dispersiva do ciclo de vida, a seleção tende a favorecer "genótipos generalistas" capazes de se ajustar aos diferentes ambientes que o dispersor pode encontrar, ao invés de genótipos localmente adaptados (Thibert-Plante & Hendry 2011, Nonaka et al. 2015). Terceiro, a reprodução sexuada permite a eliminação de mutações durante a meiose e tende a misturar alelos entre genótipos, novamente limitando a diferenciação dentro e entre populações (Gorelick & Heng 2011).

Por outro lado, há um número crescente de exemplos empíricos de que incompatibilidades reprodutivas podem evoluir por seleção divergente em apenas algumas dezenas de gerações (Hendry, Nosil & Rieseberg 2007), e mesmo na presença de fluxo gênico (Ollerton 2005). Além disso, a pesquisa recente sugere que a plasticidade fenotípica pode na verdade facilitar este processo, uma vez que ela permite que a composição fenotípica das populações mude rapidamente perante um novo ambiente (Lande 2015). Dado que as novas condições ambientais sejam estáveis, a seleção pode deixar de favorecer a plasticidade, levando à eventual fixação de um fenótipo originalmente plástico. Este processo, no qual o fenótipo "guia" os genes (e não o contrário), é conhecido como "assimilação genética", e pode estar envolvido em muitos casos de adaptação rápida e especiação ecológica (Lande 2015, Nonaka et al. 2015). Finalmente, embora a teoria contemporânea de especiação enfatize a evolução de incompatibilidades reprodutivas, estima-se que cerca de 9000 espécies eucarióticas sejam partenogenéticas (i.e. gerem prole sem fertilização) (Simon *et al.* 2003; Mora *et al.* 2011), muitas das quais descendem de ancestrais igualmente partenogenéticos datados de dezenas a centenas de milhões de anos (Schön, Martens & van Dijk 2009). Em grupos proximamente relacionados, há evidência de que a taxa de especiação tende a ser maior entre espécies assexuadas, possivelmente devido à ausência dos efeitos homogeneizantes do sexo sobre o genoma (Gorelick & Heng 2011; Tang *et al.* 2014). Assim, a seleção poderia ser ainda mais importante na especiação de populações clonais.

Embora haja 105 filos reconhecidos (Margulis & Chapman 2009), duas em cada três espécies descritas pertencem a apenas um deles, Arthropoda (Grimaldi & Engel 2005). Grande parte desta diversidade ocorre nos solos, incluindo a serrapilheira (Giller 1996; Basset *et al.* 2015). Neste ambiente, a vida animal é sustentada por detritos vegetais, dando origem a "teias tróficas marrons". A estrutura destas teias molda o funcionamento dos ecossistemas, afetando tanto plantas quanto consumidores de seus tecidos vivos (Hagen *et al.* 2012). Em um metro quadrado de solo, frequentemente coexistem algumas centenas de espécies de artrópodes – um "enigma" que desafia o princípio de exclusão competitiva (Anderson 1975). Curiosamente, espécies partenogenéticas, especialmente de ácaros e colêmbolos, parecem ser mais comuns no solo que em outros ambientes (Scheu & Drossel 2007). Acredita-se que a coexistência entre espécies edáficas reflita, em parte, a grande heterogeneidade física desse substrato (Bardgett 2002; Decaëns 2010). Entretanto, uma questão ainda mais geral persiste: de onde vieram tantas espécies? Em comunidades acima do solo, como as de insetos fitófagos, há evidência de que até 44% das espécies estão em processo de divergência adaptativa (Stireman, Nason & Heard 2005). No entanto, insetos fitófagos dependem fortemente de suas plantas hospedeiras, o que poderia facilitar o isolamento parcial entre populações habitando hospedeiros diferentes. Já em um substrato espacialmente contínuo como o solo, esta diferenciação não é tão óbvia.

Em florestas neotropicais, estima-se que haja, em média, cerca de 18.000 espécies de artrópodes por hectare (Basset *et al.* 2012) – mais que o número total de espécies de árvores da Amazônia (ter Steege *et al.* 2016). Comparações entre grandes ecossistemas (i.e. floresta de terra firme vs. igapó e várzea) revelam fortes contrastes na composição de espécies das comunidades e, em alguns casos, divergência intraespecífica (Adis & Junk 2002). Entretanto, mesmo florestas de terra firme – as quais cobrem a maior parte da bacia amazônica – são recortadas por densos sistemas de drenagem, resultando em um mosaico de platôs (i.e. terras altas) e vales ou baixios (i.e. planícies ripárias). Esta variação afeta o risco de alagamento, a granulometria e a composição química do solo, influenciando assim a flora e a fauna (Costa *et al.* 2015). Por exemplo, vários estudos indicam que a topografia controla a diversidade e a composição de espécies de artrópodes edáficos em paisagens de terra firme (Oliveira *et al.* 2009; Moraes *et al.* 2011; Tarli *et al.* 2014), mas pouco se sabe sobre o quanto esta heterogeneidade promove divergência fenotípica intraespecífica.

Nesta tese, propomos que a história de vida característica dos artrópodes, combinada à heterogeneidade topográfica, favorece a divergência fenotípica nos solos em extensões espaciais relativamente pequenas. O tamanho reduzido desses animais limita sua dispersão ativa (Lehmitz *et al.* 2012), ao mesmo tempo em que aumenta a chance de dispersão passiva (Costa *et al.* 2013). Isto favoreceria a formação de adensamentos locais ligados por migração esporádica, ou "simpatria de mosaico" (Mallet *et al.* 2009). Na presença de hábitats contrastantes, isto poderia dirigir a divergência fenotípica entre populações – seja por plasticidade, seja por adaptação local –, talvez em extensões espaciais tão pequenas quanto algumas dezenas de metros (Adis & Junk 2002; Ollerton 2005; von Saltzwedel *et al.* 2014). O ciclo de vida tipicamente curto dos artrópodes favoreceria este processo, ao permitir altas taxas evolutivas. Em populações clonais, livres do efeito homogeneizante do sexo, este processo poderia ser ainda mais eficaz.

Para investigar esta questão, usamos o ácaro edáfico *Rostrozetes ovulum* (Berlese, 1908) (Acari: Oribatida) (Figura 1a). Ácaros são numericamente dominantes nos solos de florestas do mundo todo, atingindo densidades de 10^5 indivíduos m^{-1} (Petersen & Luxton 1982). *R. ovulum* é cosmopolita, mas atinge maiores densidades em florestas tropicais (> 10^3 indivíduos m^{-1}) (Pequeno *et al.* 2017). Como a maioria dos artrópodes edáficos, *R. ovulum* tem um tamanho diminuto (ca. 0,3 – 0,4 mm de comprimento), se alimenta de detritos vegetais, e tem mobilidade extremamente baixa. Para visualizar melhor a percepção espacial deste animal, considere um indivíduo de 340 μm de comprimento. Se ele fosse do tamanho de um cão labrador (uma raça comum em todo o mundo, ca. 80 cm do nariz à cauda), uma distância de 45 cm seria equivalente a 1 km, e 1 km seria equivalente a 2352 km (aproximadamente a distância entre Manaus, AM e Belo Horizonte, MG). Além disto, *R. ovulum* é uma das cerca de 1000 espécies de ácaros oribatídeos que se reproduzem por partenogênese, sendo todos os indivíduos fêmeas (Norton & Palmer 1991). Ao eclodir do ovo, cada fêmeas leva cerca de dois meses para amadurecer, produzindo clones durante os dois ou três meses seguintes (Beck 1969). Embora possam viver por mais de um ano em laboratório (Beck 1969), a longevidade em campo provavelmente é bem menor devido à mortalidade extrínseca. Paralelamente, há grande variação morfológica e fisiológica entre adultos de *R. ovulum* ocorrendo no mesmo local, mas as razões são desconhecidas (Beck 1969; Pequeno & Franklin 2014). Tais características fazem desta espécie um bom modelo para investigar divergência ecológica em simpatria.

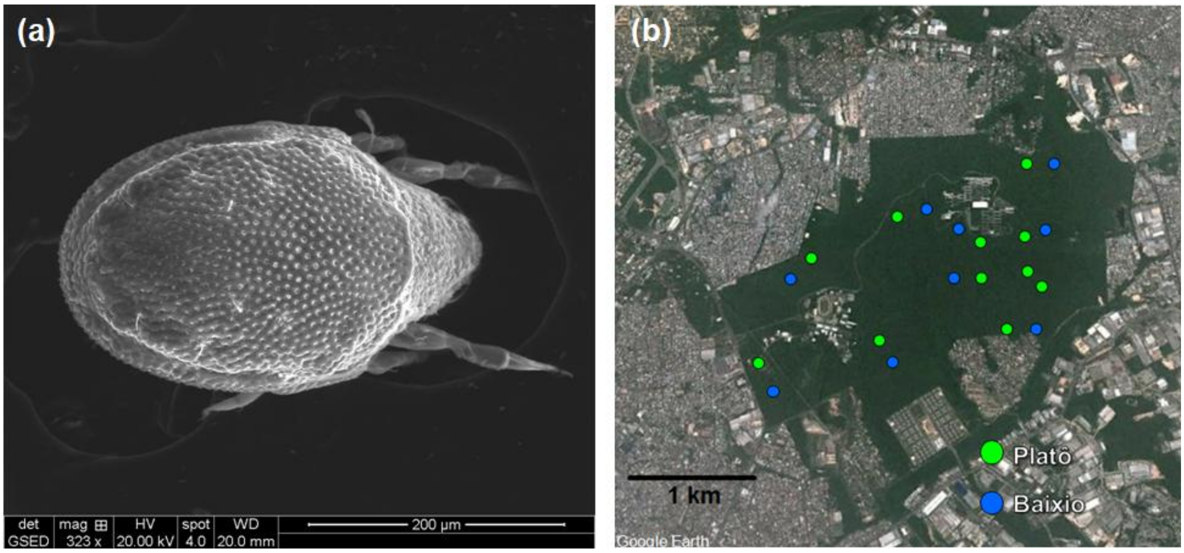

Figura 1. O sistema estudado nesta tese. (a) O ácaro oribatídeo *Rostrozetes ovulum* (Berlese, 1908), em vista dorsal. Como na maioria dos ácaros oribatídeos, o corpo de *R. ovulum* é dividido em duas partes: o proterossoma, a porção anterior contendo as peças bucais e os dois primeiros pares de pernas, e o histerossoma, a porção posterior contendo os dois últimos pares de pernas e demais órgãos. (b) Distribuição dos pontos de coleta na área de estudo, o fragmento florestal do campus da Universidade Federal do Amazonas (Manaus, AM).

Estudamos populações de *R. ovulum* distribuídas entre platôs e baixios em um fragmento florestal urbano (800 ha) na Amazônia central (Figura 1b). Em particular, avaliamos o quanto a diferença de risco de alagamento entre estes ambientes poderia atuar como agente seletivo – um fator ambiental ao qual organismos relativamente pequenos e sedentários como animais edáficos são expostos com frequência. Neste caso, esperamos que cada hábitat favoreça fenótipos com diferentes tolerâncias à submersão, afetando assim a composição fenotípica e a dinâmica das populações. Esta ideia foi testada à luz de três temas complementares (distribuição, forma e função), organizados em quatro capítulos. No capítulo 1, examinamos o padrão de variação espaço-temporal da abundância de *R. ovulum*, fornecendo o contexto ecológico necessário aos capítulos seguintes. No capítulo 2, investigamos a dinâmica populacional de *R. ovulum* em relação à composição fenotípica e ao hábitat das populações, forjando um elo entre variação populacional e individual. Nos capítulos 3 e 4, testamos diretamente o papel do risco de submersão como agente de seleção divergente entre hábitats – no primeiro caso, em termos do grau de plasticidade fenotípica do tamanho corporal, e no segundo caso, em termos de morfologia e tolerância à submersão.

OBJETIVOS

Nesta tese, avaliamos o papel da heterogeneidade de hábitat (platô vs. baixio) típica das florestas de terra firme da Amazônia como causa de divergência na dinâmica e composição de populações de um artrópode edáfico representativo, o ácaro *Rostrozetes ovulum*.

Capítulo 1: Quantificar a magnitude da variação espacial e temporal na abundância de *R. ovulum*, bem como sua relação com o hábitat e com a sazonalidade climática.

Capítulo 2: Determinar os efeitos diretos e indiretos de características ecológicas intrínsecas (i.e. tamanho corporal) e extrínsecas (i.e. hábitat) sobre a dinâmica populacional (taxa intrínseca de crescimento e força da denso-dependência) e a distribuição espacial resultante.

Capítulo 3: Testar o efeito do risco de submersão do hábitat sobre o grau de plasticidade sazonal do tamanho corporal.

Capítulo 4: Testar o efeito do risco de submersão do hábitat sobre a morfologia e a tolerância à submersão, bem como a relação entre estes atributos fenotípicos, independentemente da contribuição da migração (distância geográfica entre populações) para a diferenciação fenotípica.

CAPÍTULO 1

Spatial abundance pattern of a common soil arthropod changes suddenly with season in a tropical rainforest

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Spatial abundance pattern of a common soil arthropod changes suddenly with season in a tropical rainforest

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ABSTRACT

Species abundance is a fundamental ecological descriptor. However, spatial and temporal dimensions of abundance are often studied separately. Thus, the primacy of spatial vs. temporal factors in determining abundance, as well as the extent to which spatial patterns change over time, remains uncertain. Soil organisms are well-suited to address these issues, as they are abundant, short-lived and highly responsive to environmental variation. Here, the widespread soil mite *Rostrozetes ovulum* was used to investigate landscape-level spatiotemporal variation in abundance in an Amazonian rainforest. The species was sampled nine times over a year in 20 transects distributed between plateaus and valleys. Then, we partitioned the variance in abundance between space, time and their interaction; tested the common assumptions that spatial patterns are constant through time and temporal patterns are constant across space; tested whether abundance was seasonal; and tested whether variation in abundance reflected spatiotemporal environmental heterogeneity. *R. ovulum*'s abundance varied more in time than in space, and abundance time series from different locations were generally correlated and seasonal. However, the spatial pattern of abundance changed over the year: abundance was higher in plateaus relative to valleys, but only in the few, drier months; in wetter months, plateaus and valleys converged towards low abundance. Our results show that species distributions can be highly dynamic even in sheltered, tropical forest soils, so that conclusions on the drivers of observed distributions can change between close sampling times.

1. Introduction

The abundance of organisms varies in space and time, and it is a major goal of ecology to determine the causes and consequences of such variation (Scheiner and Willig, 2008). On the one hand, understanding the causes of abundance patterns is essential for the elaboration of effective strategies of management and conservation of biodiversity, especially in light of the uncertainties regarding species responses to ongoing climate change (Dawson et al., 2011). On the other hand, abundance variation itself can have important ecological consequences. For instance, spatiotemporal variability in abundance can weaken species interactions, thus alleviating competition and promoting species coexistence (Angert et al., 2009).

Spatial and temporal dimensions of abundance often have been approached as separate subjects, e.g. population limitation vs. population regulation, respectively (Krebs, 2002). Often, researchers make inferences about abundance patterns based on (1) single-visit, "snapshot" spatial samples or (2) single-site time series. This rests on the (often implicit) assumptions that observed spatial patterns are constant over time and that temporal patterns are constant over space, which in many cases remains untested. On the one hand, some degree of synchrony in abundance fluctuations across space seems to be relatively common in animals and plants (Bjørnstad et al., 1999). On the other hand, spatial abundance patterns appear to be more dynamic, at different spatial and temporal scales (Bishop et al., 2014; Ettema et al., 1998; Lively et al., 1993; Plein et al., 2013; Wu et al., 2014). However, little is known about how much variation in a species' abundance is attributable to either space or time, and to what extent the two interact (Legendre et al., 2010). These issues are important because they affect our understanding of ecological phenomena, e.g. the relative importance of niche vs. neutral processes (Laliberté et al., 2009) or how prone are natural assemblages to climate change (Basset et al., 2015).

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Soil organisms (including those dwelling in litter) are useful for addressing these issues as they are often abundant, short-lived and highly responsive to environmental heterogeneity (Giller, 1996). At higher latitudes, there is evidence that the abundance of soil organisms changes more over seasons than across sites within seasons (Berg and Bengtsson, 2007; Wu et al., 2014), and that their spatial patterns can change between seasons (Bishop et al., 2014; Wu et al., 2014). This suggests that climate is important in shaping spatial abundance patterns of such organisms. In the tropics, one could expect little seasonal variation given the relatively stable climate, particularly in sheltered soils of tropical rainforests (Beck, 1969). Nonetheless, rainfall is often seasonal in such ecosystems, and seasonal abundance patterns in soil fauna have been documented several times in tropical forests worldwide, even in wetter ones (Burgess et al., 1999; Frith and Frith, 1990; Levings and Windsor, 1985; Lieberman and Dock, 1982; Wiwatwitaya and Takeda, 2005).

Seasonal variation in tropical forests occurs over landscapes characterized by dense drainage systems where valleys and plateaus alternate, which creates much environmental heterogeneity (Castilho et al., 2006; Luizão et al., 2004). This heterogeneity has been shown to affect the abundance of several soil taxa (Kaspari and Weiser, 2000; Moraes et al., 2011; Tarli et al., 2014), but the extent to which it interacts with temporal variation in soil populations is little known. Yet, some studies suggest that seasonal variation among arthropod assemblages (including soil dwellers) is higher than spatial variation in tropical forests, perhaps even higher than in temperate forests (Basset et al., 2015; Medianero et al., 2007). Thus, it is possible that spatial abundance patterns of soil fauna change considerably over seasons even in tropical forests.

The parthenogenetic oribatid mite *Rostrozetes ovulum* (Berlese, 1908) (= *R. foveolatus* Sellnick) is a cosmopolitan soil dweller, occurring from peat bogs and warm-temperate forests in eastern North America (Norton and Palmer, 1991) to high moors in Japan (Kuriki and Yoshida, 1999). However, it is in tropical forests that *R. ovulum* reaches highest abundance, typically dominating oribatid assemblages (Ferreira et al., 2012; Hasegawa et al., 2014; Moraes et al., 2011; Noti et al., 1996). Like many soil arthropods, *R. ovulum* feeds on leaf litter (Illig et al., 2005), is rather small (200–500 mm long) and has limited dispersal capacity (Lehmitz et al., 2012). Thus, populations are virtually sessile and likely to be strongly affected by local/current environmental conditions at scales of a few hundred meters (Ponge and Salmon, 2013). Moreover, it has been suggested that the abundance of parthenogenetc species such as *R. ovulum* is mainly regulated by density-independent processes, so that it should fluctuate more than that of sexual species (Bluhm et al., 2016). These features render *R. ovulum* a good model for unraveling the spatiotemporal dynamics of soil fauna abundance. Here, we performed a comprehensive analysis of abundance variation in this species across the landscape and over the year in a tropical rainforest in central Amazonia. Specifically, we tested: (1) whether temporal variation in abundance is higher than spatial variation, and whether they interacted; (2) the common (yet often implicit) assumptions that spatial patterns are constant over time and that temporal patterns are constant over space; (3) whether temporal variation in abundance is seasonal; and (4) whether variation in abundance is related to two key sources of spatial and temporal environmental heterogeneity: habitat (valley or plateau) and rainfall.

2. Materials and methods

2.1. Study site

This study was conducted in a large remnant of non-flooded or *terra firme* forest (800 ha) in Manaus, northern Brazil, of which 592 ha belong to the Federal University of Amazonas State (03°04′34″S; 59°57′30″W). Altitude varies from *ca.* 60 to 120 m asl. This creates an alternation between plateaus, where water table is deep and soils are clayish, and valleys, where water table is near ground level and soils are sandy (Hodnett et al., 1997a,b). Vegetation is mostly primary rain forest, with some portions of secondary forest as well as minor cultivated areas. Forests in the region typically feature a canopy 35–40 m tall with some emergent trees, and an understory dominated by stemless palms in plateaus, and arborescent palms and herbs in valleys (Guillaumet, 1987). Mean monthly air temperature varies from 24 to 27 °C, and annual rainfall is 2200 mm, with a drier season (monthly rainfall below 100 mm) from July to September (Luizão et al., 2004).

2.2. Mite sampling

Field work was carried out from June 2014 to June 2015. We established 20 sampling transects across the forest landscape, each being 20 m long. Ten transects were located in valleys, along the margins of streams, while remaining transects were located at least 150 m away from any stream, on plateaus. Spatial coordinates (latitude and longitude in UTM) were obtained *in situ* for each transect with a GPS. Transects were sampled on nine occasions over one year (June to September and November 2014; and January, March, April and June 2015). On each occasion, sampling took two days to complete. At each transect, one soil sample was taken each meter using an aluminum soil corer (3.5 × 3.5 × 5 cm), for a total of 20 samples (or 245 cm^2) per transect. Each five consecutive samples were pooled in a single plastic container to facilitate further processing. This material was taken to laboratory, where the soil fauna was extracted into 95 percent alcohol using a modified Berlese-Tullgren apparatus (Franklin and Morais 2006). The extracted material was surveyed under a stereomicroscope for adult individuals of *R. ovulum*, which were identified using a key for *Rostrozetes* (Balogh and Balogh, 1990), counted and preserved in 95 percent alcohol. Immatures were not considered due to current difficulties in assigning them to species (Norton and Behan-Pelletier, 2009). In all analyses, individual observations consisted of mite counts per transect (or 245 cm^2) per time (n = 20 transects × 9 times = 180). However, to facilitate comparison with other studies, counts were extrapolated to a square meter and reported as such throughout the text.

2.3. Data analysis

All reported analyses were performed in R 3.3.2 (R Development Core and Team, 2015), with support of packages “adespatial” (Dray et al., 2017), “ade4” (Dray and Dufour 2007) and “glmmADMB” (Fournier et al., 2012). First, we tested for the statistical significance of variance fractions in *R. ovulum*’s abundance (*i.e.* number of individuals per transect per time) attributable to space, time and their interaction. In spatiotemporal ecological surveys, usually there is a single observation for each combination of space (e.g. transect) and time (e.g. sampling time), so that there are no degrees of freedom to test for a space-time interaction. However, Legendre et al. (2010) proposed a method based on distance-based Moran’s eigenvector maps (dbMEM, previously known as Principal Coordinates of Neighbor Matrices or PCNM) that circumvents this issue. Given a set of point coordinates in space or time, one computes a matrix representing the connectivity among points, so that points farther than a threshold distance are considered disconnected; the threshold is computed as the longest edge from a minimum spanning tree connecting all points. Then, one applies Principal Coordinate Analysis to this matrix to obtain eigenvectors, which in this case are orthogonal variables describing variation patterns occurring at different scales. Eigenvectors with positive autocorrelation − typically the autocorrelation of interest in ecological studies − are then used as predictor variables in a linear model to provide a parsimonious, yet realistic representation of the main pattern of variation in the data (i.e. an eigenvector map). To test for space-time interaction, an ANOVA is performed with independent effects of space and time given by Helmert contrasts computed from their respective coordinates, and an interaction term given by the product of eigenvectors computed for spatial and temporal coordinates separately (model 5 in Legendre et al., 2010). Thu, we modeled *R. ovulum*'s abundance using this method, as implemented in R by function "stimodels" (adespatial package); spatial coordinates were latitude and longitude (UTM) at the centre of transects, and temporal coordinates were sampling months (counting from the first survey, coded as integers). The statistical significance of each term was assessed by randomizing the abundance data and computing the *F* statistic 999 times to obtain a null distribution (see Legendre et al., 2010 and the documentation of function "stimodels" in R for further details on the method).

Second, we tested whether spatial abundance patterns were correlated through time, and whether temporal abundance patterns were correlated across space. To this aim, we used Dray's (2008) test of dimensionality. Dray's method employs Principal Component Analysis (PCA) on standardized data (i.e. zero mean and unit variance) to determine the number of dimensions necessary to account for the underlying structure of the data. If abundance patterns are constant, then abundance should be highly collinear in space and time, so that the dimensionality of the data could be reduced without significant loss of information; the higher the number of dimensions required, the higher the variability. The method works by applying permutations tests to each principal component (PC) to assess its information content, beginning from the first one. The first uninterrupted sequence of significant PCs is retained; if the first PC is not significant, no reduction in dimensionality is warranted. *P* values are adjusted according to a sequential Bonforreni correction to account for the multiple, non-independent tests. We performed two such tests: one on abundance time series from different transects as variables, to test for their synchrony, and another on spatial abundance samples from different months as variables, to test for temporal constancy. In the former case, data from three transects were excluded because abundance was zero over the entire study period.

Third, we tested for seasonality in abundance by using a generalized linear mixed model (GLMM) assuming negative binomial errors and log link (Zuur et al., 2009). The fixed component of the model included abundance as a function of month and its quadratic term, with month coded as a quantitative variable from one to 12. This parameterization is equivalent to a linearized Gaussian function, which accounts for bell-shaped patterns (Oksanen et al., 2001). Thus, if abundance is seasonal, the quadratic term should be significant. In this case, biologically meaningful parameters − i.e. maximum abundance and its timing − can be easily calculated from linearized parameters using standard formulas (Oksanen et al., 2001). In parallel, the random component of the model was given by transect as a random intercept. This both accounts for non-independence of repeated observations from the same transect, and allows for variation in intercept among transects (Zuur et al., 2009). Under a linearized Gaussian function, this is equivalent to allowing maximum abundance to vary among transects (Oksanen et al., 2001).

Lastly, we tested for environmental effects on *R. ovulum*'s abundance using a GLMM, as before. This time predictors were habitat (plateau or valley, expressing spatial environmental heterogeneity) and monthly rainfall (expressing temporal environmental heterogeneity), as well as their interaction. Rainfall data were obtained from the online database of the Brazilian Institute for Meteorology (INMET) (www.inmet.gov.br). We used data from the nearest station, which is 10 km away from the study site. Monthly rainfall was computed as the sum of daily rainfall during the 30 days immediately before each sampling.

3. Results

There was considerable patchiness in *R. ovulum*'s abundance across the landscape and throughout the year. Abundance ranged from 0 to 1755.10 individuals/m^2 per sampling time. However, over all 180 observations, abundance averaged 58.04 individuals/m^2 per sampling time. ANOVA revealed that temporal variance in abundance was twice larger than spatial variance, but the space-time interaction term was not statistically significant (Table 1). Further, PCA revealed a high degree of synchrony among abundance time series from different transects, so that the data could be meaningfully summarized by the two first PCs alone ($P = 0.008$ and 0.021, respectively). The first PC accounted for 61 percent of the variance in abundance, whereas the second PC accounted for 20 percent. In contrast, correlation among spatial abundance samples from different months was low, so that even the first PC accounted for only 34 percent of the variance in the data, which was not statistically significant ($P = 0.07$).

Table 1
ANOVA of *Rostrozetes ovulum* abundance in relation to space, time and their interaction, as modeled by distance-based Moran's eigenvector maps (dbMEM) (model 5 of Legendre et al., 2010). The threshold distance used for creating spatial and temporal dbMEM was 901.9 m and 2 months, respectively, based on the minimum spanning tree computed for each set of coordinates. Independent effects of space and time were coded as Helmert contrasts of spatial and temporal coordinates, respectively; six spatial and three temporal eigenvectors captured positive autocorrelation, and these were used to model the interaction term. Significant *P* values are in bold.

Source	df	r^2	*F*	*P*
Space	19	0.12	1.57	**0.038**
Time	8	0.24	7.47	**0.001**
Space × time	18	0.08	1.18	0.258
Residuals	134			

There was clear seasonality in *R. ovulum*'s abundance, but maximum abundance was highly variable across space (Table 2, Fig. 1). On average, abundance peaked between September and October, when it reached 71 individuals/m^2. However, random intercepts varied largely among transects, with estimates of the abundance peak varying from 19.99 to 251.83 individuals/m^2.

Spatiotemporal variation in *R. ovulum*'s abundance was strongly related to environmental heterogeneity, with habitat and rainfall predicting half of the variance (Table 2, Fig. 2). Abundance declined across space from plateaus to valleys, and over time from drier to wetter months. However, there was a strong interaction between habitat and rainfall: most temporal change in abundance occurred in plateaus, whereas in valleys abundance was consistently low throughout the year. Consequently, habitat differences were only evident during the few, drier months; in wetter months, they were negligible (Fig. 2). For instance, in the driest month (0.6 mm rainfall), abundance was nine times higher in plateaus (384.89 individuals/m^2, on average) than in valleys (43.26 individuals/m^2, on average). Conversely, in the wettest month (304.1 mm rainfall), the ratio (1.44) was much smaller, with an average of 5.30 individuals/m^2 in plateaus and 3.67 individuals/m^2 in valleys.

Table 2
Generalized mixed models of spatiotemporal variation in *Rostrozetes ovulum* abundance in a central Amazonian rainforest. Two models are presented: one for the effect of seasonality (month and its quadratic term as predictors) and another for the effect of environmental heterogeneity (habitat and rainfall as predictors). Models assumed negative binomial errors and log link, and included transect as a random intercept (ranges are given in parentheses). Habitat coefficients assumed valley as baseline.

Model	r^2	Predictor	Coefficient	*Z*	*P*
Seasonality	0.59	Intercept	−5.011 (−6.26 to −3.74)	−4.29	< 0.001
		Month	1.193	3.44	< 0.001
		Month^2	−0.064	−2.5	0.012
Environment	0.53	Intercept	0.069 (−0.63 to 1.35)	0.18	0.85
		Habitat	2.183	4.60	< 0.001
		Rainfall	−0.008	−4.38	< 0.001
		Habitat × Rainfall	−0.006	−2.50	0.012

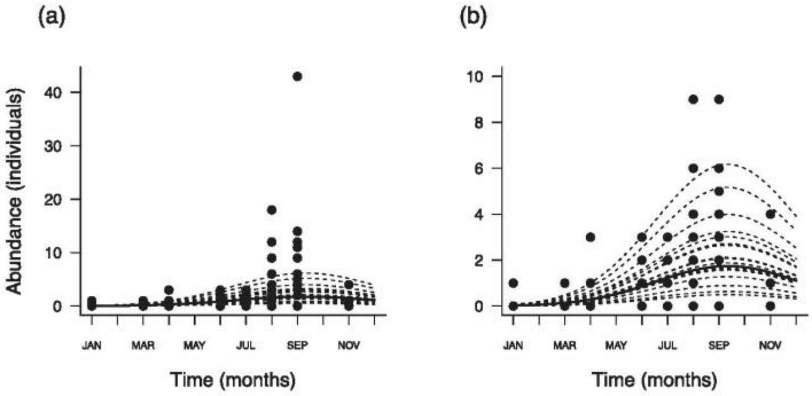

Fig. 1. Seasonality in the abundance of the soil mite *Rostrozetes ovulum* in a central Amazonian rain forest. (a) All data. (b) Same plot, but zoomed in on the concentration of data for better visualization. Each point represents a transect/sampling time combination. Lines represent GLMM fits based on parameters given in Table 2. The thicker line represents the overall, average fit (fixed component), while dotted lines indicate transect-specific fits (random component).

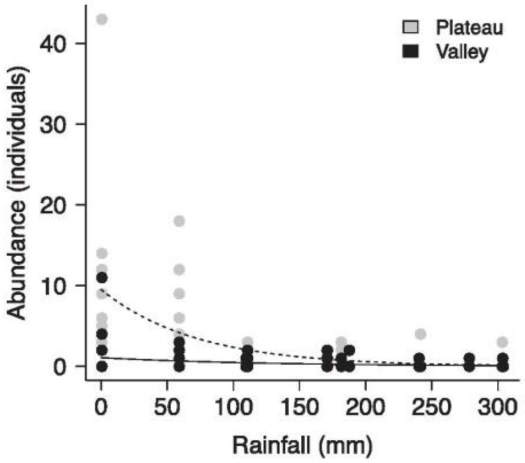

Fig. 2. Spatiotemporal variation in the abundance of the soil mite *Rostrozetes ovulum* in relation habitat (plateau or valley) and rainfall in a central Amazonian rain forest. Rainfall was calculated for the period of a month immediately before each sampling time. Each point represents a transect/sampling time combination. Lines represent GLMM fits based on the fixed model parameters given in Table 2.

4. Discussion

This study revealed that the abundance of a common soil arthropod, the oribatid mite *Rostrozetes ovulum*, varied more in time than in space in a tropical rainforest landscape. This agrees with other studies that assessed both spatial and temporal sources of variation in soil fauna abundance (Basset et al., 2015; Berg and Bengtsson, 2007; Medianero et al., 2007; Wu et al., 2014), although this is the first time, to our knowledge, that a direct partitioning of variance has been provided. However, while temporal abundance patterns from different locations were mostly synchronized and seasonal, spatial abundance pattern was variable through time. Further, this pattern was related to environmental factors: abundance declined nonlinearly from wetter to drier months, and from plateaus to valleys. Thus, overall, our results suggest that inferences from spatially-oriented studies are prone to higher uncertainty than those from time series studies. However, temporal variation in spatial pattern can be substantial, even if it is predictable. Therefore, ignoring either space or time could lead to biased inferences. We stress that these conclusions refer to the spatial and temporal scales studied here (i.e. intra-annual variation across several kilometers). Nonetheless, seasonal change in spatial abundance patterns has been shown at other scales and regions for soil nematode species (Ettema et al., 1998) and for higher taxa of springtails and mites (Wu et al., 2014), suggesting that this might be a common feature of soil fauna.

The annual peak in *R. ovulum*'s abundance is in line with the view that soil fauna is seasonal in tropical forests (Burgess et al., 1999; Frith and Frith, 1990; Levings and Windsor, 1985; Lieberman and Dock, 1982; Medianero et al., 2007; Wiwatwitaya and Takeda, 2005). A similar pattern also was found for *R. ovulum* in the Amazonian floodplain, although there the abundance peak coincided with the terrestrial phase of the flood cycle (Beck, 1969). The pattern of intra-annual fluctuations in abundance reflects in part the number of generations (Adis and Junk, 2002). In the laboratory, *R. ovulum* individuals can live for over a year (Beck, 1969; Messner et al., 1992), but given the different environmental conditions this has unknown relevance to longevity in nature. Actually, average lifespan is likely to be shorter in the field, as individuals are probably exposed to higher mortality.

The high patchiness in *R. ovulum*'s abundance caused seasonality to be more evident at relatively few locations; when averaged over the landscape, the seasonal pattern was modest (Fig. 1). This means that a time series from a random location would likely underestimate abundance seasonality, e.g. would make it look aseasonal. On the other hand, pooling data from different locations (e.g. summing abundances) into a single time series to simplify temporal analysis would mask the patchiness in abundance, thus running the risk of overestimating seasonality. Because the abundance of soil organisms is typically patchy (Ettema and Wardle, 2002), this finding is likely to be relevant for other soil species and landscapes.

Seasonal variation in *R. ovulum*'s abundance correlated with rainfall, so that individual counts decreased suddenly as rainfall increased. This result suggests high susceptibility of this species (and perhaps other soil dwellers) to the effects of climate change. Accordingly, there is evidence that changes in rainfall can have a stronger effect on soil organisms than factors such as temperature and CO_2 (Kardol et al., 2011), and that the effect is greater on soil fauna of forests than of other ecosystems (Blankinship et al., 2011). However, the abundance-rainfall relationship differed between habitats: abundance decreased markedly with rainfall in plateaus, but was consistently low and virtually constant throughout the year in valleys. A decrease in *R. ovulum*'s abundance (as well as of overall oribatid mite abundance) from highland towards lowland habitats has also been reported for North America (Donaldson, 1996) and Japan (Kuriki and Yoshida, 1999), suggesting a consistent relationship across biogeographic regions. Yet, the decrease in abundance with rainfall contradicts the generally positive correlation between soil fauna abundance and rainfall reported in the literature (Burgess et al., 1999; Frith and Frith, 1990; Levings and Windsor, 1985; Lieberman and Dock, 1982; Wiwatwitaya and Takeda, 2005), suggesting that a different mechanism might be in place.

Rainfall and habitat correlate with several environmental properties in central Amazonia that could affect *R. ovulum*'s abundance. For instance, litter tends to accumulate more in plateaus than in valleys (Luizão et al., 2004), and during drier rather than wetter months (Martius et al., 2004). Thus, the higher abundance of *R. ovulum* in plateaus relative to valleys during drier months may reflect higher litter density, either through higher food density (Illig et al., 2005), more shelter against predators (Kalinkat et al., 2013), or both. In parallel, valleys are more likely to waterlog than plateaus due to proximity to the water table, especially during rainier months (Hodnett et al., 1997a, 1997b). Thus, lower *R. ovulum* abundance in wetter sites (valleys) and times (rainier months) may also result from mortality due to waterlogging, as suggested by other studies (Levings and Windsor, 1985; Frith and Frith, 1990; Baccaro et al., 2013).

More generally, the high temporal variability in *R. ovulum*'s abundance might partly reflect its parthenogenetic reproduction. The Structured Resource Theory of Sexual Reproduction suggests that parthenogenetic species are favored by high resource density and high mortality rate over sexual ones (Scheu and Drossel, 2007). If so, then the abundance of parthenogenetic species would be mainly regulated by density-independent (as opposed to density-dependent) factors, thus resulting in high temporal variability in abundance (Bluhm et al., 2016). Indeed, density-independent mortality (i.e. flooding) seems to be the main cause of extrinsic mortality in *R. ovulum* populations inhabiting floodplains (Pequeno and Franklin, 2014). Nonetheless, it remains to be determined whether the same applies to *R. ovulum* populations from non-flooded forest, as studied here, and whether the observed level of temporal variability in abundance exceeds that of co-occurring, sexual oribatid mites.

In conclusion, we have shown that the spatial abundance pattern of the common soil mite *R. ovulum* changed markedly over a year in a tropical rainforest. Moreover, this change was related to environmental heterogeneity in both space and time. This indicates that inference on abundance patterns of soil fauna can change drastically between different sampling times within the same year, and suggests that soil populations are highly susceptible to the effects of climate change. Comparison with previous literature suggests that these conclusions might be valid to soil fauna in general. We suggest that both spatial and temporal dimensions should be considered when assessing soil fauna abundance and its drivers.

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CAPÍTULO 2

Disentangling the effects of population dynamics, phenotype and environment on species distribution

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Em revisão em *Journal of Animal Ecology*

Abstract

1. Heterogeneous species distributions partly reflect spatial variation in population dynamic parameters, which are themselves summaries of phenotypic and environmental effects. Yet, the relationship between such parameters is unclear, as is the extent to which they translate phenotypic and environmental effects into spatial variation in population density.

2. We investigated the direct and indirect contributions of population dynamic parameters, phenotype and habitat to spatial variation in mean population density, using the cosmopolitan soil mite *Rostrozetes ovulum*.

3. We assessed year-round density fluctuations and mean adult body mass – a key life-history trait – of populations from plateaus and valleys across a tropical rainforest landscape. We employed numerical simulations to estimate intrinsic growth rate and strength of density dependence from density fluctuations while accounting for known sources of bias. Then, we used structural equation modelling to quantify the effects of mean body mass and habitat on mean density, both directly and indirectly (through population dynamic parameters).

4. *R. ovulum*’s mean density decreased with stronger density dependence and from plateaus to valleys, but increased with mean body mass. Such effects were direct rather than indirect, with those of density dependence and body mass being slightly stronger than that of habitat. Further, there was some evidence that populations with higher intrinsic growth rate tended to experience stronger density dependence.

5. Our results suggest that density dependence is more important than intrinsic growth rate in shaping species distribution, although the latter may play an indirect role. Furthermore, they show that population dynamic parameters do not necessarily reflect important phenotypic and environmental effects on population density.

Key words: competition, density feedback, life history, logistic equation, *r*-*K* selection

Introduction

All species have heterogeneous distributions at some spatial scale, which is one of the earliest motivations for ecological theory (Scheiner & Willig 2008). Part of this heterogeneity can be attributed to variation in the underlying population dynamics (Post 2005; Schmitt & Holbrook 2007; Thorson *et al.* 2015), which depends itself on the phenotypic composition of populations and their aggregate response to the environment. For instance, both the intrinsic growth rate of populations and the strength of the density feedback they experience can be affected by body size, a common correlate of life history traits and competitive ability (Gaston 1988; Messina 2004; Mueller 2009; Herrando-Pérez *et al.* 2012), as well as by environmental conditions such as temperature and resource availability (Agrawal, Underwood & Stinchcombe 2004; Miller 2007; Marra *et al.* 2015; Johnson *et al.* 2016). Less clear is how and to what extent variation in population dynamic parameters shapes species distribution.

Theory suggests that, as population density (N) grows, per capita growth rate (R) generally decreases due to stronger competition, as summarized by the classic logistic equation (Kuno 1991; Mallet 2012; Arditi, Bersier & Rohr 2016):

$$R = r - \alpha N \qquad \text{(Eq. 1)}$$

Here, r is the intrinsic growth rate, which describes maximum or potential per capita growth rate (i.e. in the absence of density effects), and α is the intraspecific competition coefficient, which describes how strongly density increments reduce per capita growth rate. Although details of the equation can vary (e.g. continuous vs. discrete time, N vs. $\log N$), r and α summarize density-independent (e.g. abiotic conditions) and density-dependent effects (e.g. competition) on population dynamics, respectively. Under equilibrium density (i.e. $R = 0$), $N = r/\alpha$, also known as the "carrying capacity" (K). Thus, theory suggests that equilibrium density should be proportional to intrinsic growth rate and inversely proportional to strength of density dependence (Kuno 1991; Mallet 2012; Arditi *et al.* 2016). Even if populations are never in perfect equilibrium, one would still expect mean density to relate similarly to such parameters, but the relative contributions of each to heterogeneity in species distribution are poorly known (Hart & Gotelli 2011; Mallet 2012; Wetzel 2014).

In principle, the logistic model treats r and α as independent. Yet, the classical theory of r-K selection predicts that, as density increases, selection should favour individuals less affected by competition (i.e. weaker density dependence, higher carrying capacity) at the expense of lower reproductive rate (i.e. lower intrinsic growth rate), assuming these functions trade off (MacArthur & Wilson 1967; Reznick 2014). In light of eq. 1, this implies that α should increase with r, so that K would decrease with the latter (Kuno 1991; Mallet 2012). However, to the extent that $K = r/\alpha$, higher r should increase, not decrease K. Alternatively, a correlation between r and α could also arise due to environmental effects, e.g. if higher resource supply increases intrinsic growth rate so as to foster crowding and density dependence (Bell 1990; Jasmin & Zeyl 2012). Many studies have assessed the relationship between r and K, but few have directly addressed the relationship between r and α (Agrawal *et al*. 2004; Mallet 2012). Thus, the relationship between fundamental population dynamics parameters remains unclear.

Soil animals are notable for their high species density and highly patchy species distributions (Ettema & Wardle 2002). In contrast, their population dynamics has been seldom investigated under natural conditions (Ferguson & Joly 2002; Kampichler & Geissen 2005; Uvarov 2017). Because soil animals are generally small-bodied, short-lived and relatively sessile, there is much potential for phenotypic and genetic differentiation among populations at distances as short as a hundred meters or less (Palmer & Norton 1992; von Saltzwedel *et al.* 2014), which could result in variation in population dynamics. Thus, soil animals provide a good opportunity for gaining new insights into the links between species distribution, population dynamics, phenotype and environment.

Here, we investigated this issue with a widespread soil arthropod, the mite *Rostrozetes ovulum* (Berlese, 1908) (Oribatida: Haplozetidae). We repeatedly sampled populations distributed between contrasting habitats (i.e. plateaus and valleys) across a tropical rainforest landscape over a year. Next, we estimated their mean adult body mass – a descriptor a life-history variation – and population dynamic parameters (i.e. intrinsic growth rate and strength of density dependence) from density time series using numerical simulation to account for different sources of bias. Then, we used structural equation modelling to test for direct and indirect effects of population dynamics parameters, mean adult body mass and habitat on mean density. We hypothesized that intrinsic growth rate and strength of density dependence would affect mean density directly. In parallel, mean adult body mass and habitat would affect mean density either directly or indirectly, by affecting population dynamic parameters. Lastly, we tested for a correlation between intrinsic growth rate and density dependence.

Materials and methods

Study species

Rostrozetes ovulum (= *R. foveolatus* Sellnick) is a soil-dwelling oribatid mite with wide geographic range: it occurs from peat bogs and warm-temperate forests in eastern North America (Norton & Palmer 1991) to high moors in Japan (Kuriki & Yoshida 1999), but is especially abundant in tropical forests worldwide (Noti, André & Dufrêne 1996; Moraes *et al.* 2011; Hasegawa *et al.* 2014). The mite feeds on leaf litter (Illig *et al.* 2005), has a rather small adult body size (although variability is relatively high, i.e. 200 – 500 µm long), little mobility, and reproduces by parthenogenesis (i.e. all individuals are female clones) (Pequeno & Franklin 2014). In laboratory, individuals take around two months to reach maturity after hatching, and then lay eggs for two to three months (Beck 1969). In the field, seasonal peaks in adult abundance last between two and three months, suggesting that average adult lifespan has a similar duration (Beck 1969). Thus, two or more generations are produced yearly.

These features suggest that *R. ovulum* is likely to show significant differentiation in population characteristics at relatively small spatial extents. To better visualize the spatial setting of *R. ovulum*, consider an individual 360 µm long. If the mite were the size of a labrador retriever, a common dog breed worlwide (about 80 cm long from nose to tail base), then a distance of 45 cm would be equivalent to 1 km. Accordingly, for *R. ovulum* to travel a distance of 2 km would be roughly equivalent to cross North America from New York to San Francisco in straight line (about 4130 km).

Study site

We sampled *R. ovulum* in a large forest remnant (800 ha) in Manaus, northern Brazil, most of which belongs to the Federal University of Amazonas (03°04’34”S; 59°57’30”W). Mean monthly air temperature varies from 24 to 27 °C, and annual rainfall is 2200 mm, with a drier season (monthly rainfall below 100 mm) from July to September (Luizão *et al.* 2004). Local relief features a dense drainage system where altitude varies from *ca.* 60 to 120 m asl. This creates an alternation between plateaus and valleys, which contrast in environmental conditions. In plateaus, soils are clayish and the water table is many meter below ground level, whereas in valleys soils are sandy and the water table is shallow, thus causing waterlogging and short-term floods during heavy rains (Hodnett *et al.* 1997; Junk *et al.* 2011). Soil chemistry also varies, with plateaus having higher C and N but lower P contents than valleys (Castilho *et al.* 2006). In parallel, plateaus tend to have higher plant biomass and to produce and accumulate more litter than valleys (Luizão *et al.* 2004; Castilho *et al.* 2006).

Data sampling

We sampled 20 transects distributed over the forest landscape from June 2014 to June 2015. Each transect was 20 m long; 10 transects were in valleys, while the remaining transects were located on plateaus, at least 150 m away from any drainage catchment. Transects were sampled on nine occasions over one year (June to September and November 2014; and January, March, April and June 2015). On each occasion, sampling took two days to complete. At each transect, one soil sample was taken each meter using an aluminum soil corer (3.5 × 3.5 × 5 cm), covering a total of 245 cm^2. This material was taken to laboratory, where soil fauna was extracted into 95 percent alcohol using Berlese-Tullgren apparatus (Franklin & Morais 2006), and then surveyed under a stereomicroscope for *R. ovulum* adults. These individuals were identified using a key for *Rostrozetes* (Balogh & Balogh 1990), counted and preserved in 95 percent alcohol. We did not consider immatures given current difficulties in their species identification (Norton & Behan-Pelletier 2009). In three valley transects, no *R. ovulum* individuals were found; because estimation of population dynamic parameters depends on temporal variation in density, these transects could not be used and were excluded from further analyses. A population was defined here as all adult individuals occurring within the sampled area of a transect (245 cm^2) at any time. Because all transects had the same sampled area, we refer to counts as densities.

To estimate body mass, collected individuals were photographed under a microscope, and their body length (L) and width (W) were measured, in μm. These measurements were then used to predict body mass (M) in μg, according to the following model:

$$\log M = -17.17 + 3.00 \log (L + W) \qquad \text{(Eq. 2)}$$

This model is robust to variations in body shape, explaining 98% of the variance in adult body mass of oribatid species (Caruso & Migliorini 2009).

Statistical analyses

The following variables were computed for each population for further analyses: mean density over surveys; population dynamic parameters (i.e. intrinsic growth rate and strength of density dependence); mean adult body mass over surveys; and habitat (i.e. plateau or valley). To estimate population dynamic parameters, we used density time series (Fig. 1) to access the relationship between per capita growth rate (R) and population density (N). R was defined as the log ratio between subsequent densities, standardized by the time interval between them (Agrawal *et al.* 2004):

$$R = \frac{\log\left(\frac{N_{t+1}}{N_t}\right)}{T} \qquad \text{(Eq. 3)}$$

where t indicates a given point in time (i.e. a survey), and T is the time interval between subsequent surveys, in months (possibly a non-integer in this case). Next, we regressed R on log N_t to obtain estimates of intrinsic growth rate (i.e. intercept) and strength of density dependence (i.e. slope). This is equivalent to the Gompertz model, which allows for greater nonlinearity in the shape of density dependence than the logistic model but is still linear in its parameters, and is well supported empirically (Brook & Bradshaw 2006; Hart & Gotelli 2011; Herrando-Pérez *et al.* 2014; Thorson *et al.* 2015). To handle zeros, we used $N_t + 1$ in this and all subsequent calculations. As our sampling covered one year, our estimates refer to intra-annual dynamics.

The use of standard regression to estimate population dynamic parameters has been criticized as it tends to overestimate the strength of density dependence, and this bias increases with increasing measurement error in density (Freckleton *et al.* 2006; Knape & de Valpine 2012; Lebreton & Gimenez 2013). Further, because intercept and slope are estimated from the same time series, their null correlation differs from zero, thus biasing tests of their relationship (Agrawal *et al.* 2004). One increasingly popular alternative is to replace standard regression by state-space models, which estimate (and allegedly control for) both process and measurement error (Freckleton *et al.* 2006; Knape & de Valpine 2012; Lebreton & Gimenez 2013). However, the accuracy of such models decreases rapidly as measurement error increases (Auger-Méthé *et al.* 2016), and their parameter identifiability is low, so that estimates are even more correlated than in standard regression (Lebreton & Gimenez 2013). These shortcomings call for alternative approaches that reasonably minimize bias while still allowing for meaningful tests of the relationship between population dynamic parameters. To this aim, we employed numerical simulations.

First, we incorporated the effect of measurement error on estimates of population dynamic parameters by simulating variability in extraction efficiency of soil mites from soil samples. Published assessments indicate that Berlese-Tullgren apparatus extract oribatid mites from soil with an absolute efficiency of 75 – 100% (Andre, Ducarme & Lebrun 2002). Thus, we described extraction efficiency as a random variable with uniform distribution ranging from 0.75 to 1.00. Next, for each population, we divided each observed density (i.e. $N + 1$) by an extraction efficiency randomly drawn from this distribution to estimate real density (i.e. if extraction efficiency was lower than 1.00, real density was larger than observed one). Then, we calculated R and estimated population dynamic parameters through regression as described before. This procedure was repeated 99 times for each population, thus generating distributions for intercept (i.e. intrinsic growth rate) and slope (i.e. strength of density dependence) that reflected uncertainty in extraction efficiency. We took their means as point estimates.

Second, we accounted for the inherent bias in regression estimates of population dynamic parameters using null modelling. A plausible null model for population dynamics is obtained by setting the density dependence term in Equation 1 to zero, and allowing for stochasticity (Dennis & Taper 1994):

$$R = r + \varepsilon \qquad \text{(Eq. 4)}$$

where ε stands for random deviations. Thus, population dynamics is assumed to be density-independent: if $r = 0$, the population is expected to go through a random walk, otherwise it tends to grow ($r > 0$) or shrink ($r < 0$) exponentially. For each population, we simulated null dynamics in two stages. The first stage was as follows:

(1) real densities were estimated from observed densities and used to calculate R, as before;

(2) R was modelled as a normal distribution with mean (i.e. r) and standard deviation (i.e. ε) estimated from the calculated values;

(3) population density was projected through time according to Equation 4, beginning from the first observed density and for the same number of surveys (i.e. nine time steps). Projected densities were rounded down to convert to counts as the original data;

(4) R was recalculated from this simulated time series and used to estimate population dynamic parameters through regression, as before.

This procedure is equivalent to the protocol of Dennis and Taper (1994) for obtaining bootstrapped confidence intervals for population dynamic parameters. The only difference is that, instead of bootstrapping parameters, we applied it to the null model to infer parameter null distributions. This procedure was repeated 99 times for each population to simulate variability in extraction efficiency under the null model, and the means of the resulting intercept and slope distributions were taken as point estimates. The second stage consisted of repeating this entire process 499 times, thus generating a null distribution for each parameter while accounting for imperfect extraction efficiency.

Estimates of population dynamic parameters adjusted for extraction efficiency (*observed*) were compared to their respective null distributions (*null*) to obtain Standardized Effect Sizes (*SES*):

$$SES = \frac{observed - \overline{null}}{sd(null)} \qquad \text{(Eq. 5)}$$

SES are unbiased parameter estimates under a specified null model (Swenson 2014), and were used in all subsequent analyses. Positive values indicate deviation above the null expectation, whereas negative values indicate the opposite. We tested whether the mean SES of each population dynamic parameter differed from null expectation (i.e. zero) with one sample *t* tests.

To test for the effects of mean body mass and habitat on mean density, both direct and indirect (through SES of population dynamic parameters), we employed piecewise structural equation modelling (SEM) (Lefcheck 2016). Piecewise SEM extends standard path analysis to allow an assessment of the goodness-of-fit of the global structural model. This is performed by using Fisher's *C* statistic to test the hypothesis that all variables are conditionally independent. Thus, accepting the null hypothesis here ($P > 0.05$) means that the global structural model is statistically supported. Habitat (i.e. plateau or valley) was coded as a dummy variable, and mean adult body mass and mean density were log-transformed to linearize relationships.

Lastly, to test for an association between the SES of intrinsic growth rate and strength of density dependence, we used Spearman's rank correlation. All analyses were performed in R 3.3.2 (R Development Core Team 2017) using standard functions.

Results

There was substantial variation in both density and adult body mass across *R. ovulum* populations. Mean density varied one order of magnitude, ranging from 0.1 to 5.2 individuals per transect, or 4.2 to 197 individuals m^{-1}. The same occurred with mean adult body mass, which varied from 3.4 to 11.13 µg.

The simulations showed that the known uncertainty in extraction efficiency had little impact on estimates of strength of density dependence: slopes based on the raw data averaged

0.61 ± 0.26 (mean ± SD), whereas those adjusted for imperfect extraction efficiency averaged 0.61 ± 0.25. In contrast, estimates of intrinsic growth rate tended to be larger after accounting for imperfect extraction efficiency: intercepts based on the raw data averaged 0.36 ± 0.16, whereas adjusted intercepts averaged 0.44 ± 0.16.

Accounting for bias in parameter estimation through null modelling revealed that there was no tendency for intrinsic growth rate to depart from null expectation ($t = 0.19$, $P = 0.85$). However, the strength of density dependence tended to be significantly larger than expected by chance ($t = 2.89$, $P = 0.01$) (Fig. 2).

Mean density was not affected by intrinsic growth rate ($t = 0.17$, $P = 0.87$; Fig.3a). However, it decreased as density dependence became stronger ($t = -2.92$; $P = 0.01$; Fig. 3b), increased with mean adult body mass ($t = 3.37$, $P = 0.005$; Fig. 3c), and decreased from plateaus to valleys ($t = -2.62$; $P = 0.02$; Fig. 3d). These effects accounted for over half of the variance in mean density. In contrast, mean body mass and habitat explained neither intrinsic growth rate ($t = 0.68$, $P = 0.50$ and $t = -1.95$, P = 0.07, respectively) not strength of density dependence ($t = 1.61$, $P = 0.13$ and $t = 0.45$, P = 0.66, respectively). Overall, then, our data supported a structural model (Fisher's $C = 4.59$, $P = 0.10$) according to which mean density was solely driven by direct rather than indirect effects, with those of strength of density dependence and mean body mass being slightly greater in magnitude than that of habitat (Fig. 4).

Lastly, there was a positive correlation between strength of density dependence and intrinsic growth rate, even though it was only marginally significant (Fig. 5).

Discussion

Despite the central role of population dynamics in ecological theory, the mechanism through which is shapes species distribution is not well resolved. Thus, this study aimed at quantifying the direct and indirect contributions of population dynamic parameters, phenotype and habitat to heterogeneity in species distribution. We found that variation in the mean density of the soil mite *R. ovulum* across a tropical rainforest landscape was predicted by strength of density dependence, mean adult body mass and habitat, but not by intrinsic growth rate. Furthermore, all these effects were direct. Thus, population dynamic parameters proved ineffective in translating the studied phenotypic and environmental sources of variation into changes in density.

The fact that the strength of density dependence, but not intrinsic growth rate, affected mean density is in line with other reports of density-dependent population dynamics in other soil animal systems (Ferguson & Joly 2002; Kampichler & Geissen 2005; Uvarov 2017). Thus, density dependence may be a common driver of heterogeneous species distributions in soils. A tight relationship between population density and spatial heterogeneity in strength of density dependence has also been shown for plant-dwelling insects (Wetzel 2014), suggesting a commonality between below- and above-ground population dynamics. Yet, our result contradicts the positive relationships between equilibrium density and intrinsic growth rate often reported by experimental studies (Luckinbill 1978; Kuno 1991; Hendriks *et al.* 2005; Fitzsimmons *et al.* 2010). Such difference may either due to fundamental differences between population dynamics in laboratory and in nature, or because the relative contributions of population dynamic parameters to spatial variance in density vary across taxa (Hart & Gotelli 2011).

The decrease in *R. ovulum*'s mean density with stronger density dependence suggests that the distribution of this species is shaped by processes occurring at high population density relative to resource density, such as competition. It has been hypothesized that competition would be of little importance to tropical oribatid mite populations, because their densities are much smaller than those of their temperate counterparts (Maraun *et al.* 2012). More specifically, the population dynamics of parthenogenetic species such as *R. ovulum* has been proposed to be mainly driven by density-independent processes, assuming that parthenogens displace sexual species under harsh environmental conditions (Bluhm, Scheu & Maraun 2016). Our direct estimates of density dependence and its effect on mean density refute both ideas. We propose that competition is possible in tropical soil fauna because litter density and nutritional quality are highly patchy. For instance, there is evidence that contents of particular nutrients can limit soil arthropod populations in tropical forests (Kaspari & Yanoviak 2009; Tarli *et al.* 2014; Kaspari *et al.* 2017). Thus, even if population density is not as high as in temperate soils, resources may be locally limiting to the point of driving competition and, consequently, density dependence.

The fact that habitat and mean adult body mass affected *R. ovulum*'s mean density independently of strength density dependence suggests that these effects were density-independent. For instance, valleys are more likely to flood than plateaus (Hodnett *et al.* 1997; Junk *et al.* 2011), so that *R. ovulum* may experience higher extrinsic mortality rates in the former habitat. Indeed, intrinsic growth rate (the density-independent parameter of population dynamics) tended to be lower in valleys than in plateaus, although this effect was only marginally significant, and mean density was unrelated to intrinsic growth rate. Likewise, fecundity and reproductive rate increase with adult body size both within and across arthropod species (Gaston 1988; Honek 1993; Herrando-Pérez *et al.* 2012), suggesting that higher density with larger adult body size reflects higher birth rates and, thus, higher intrinsic growth rate. Again, though, the latter was not predicted by mean adult body mass nor had any effect on mean density. Thus, neither strength of density dependence nor intrinsic growth rate captured the effects of habitat and body size on mean density. This may be because intrinsic growth rate implicitly combines two rates (i.e. birth and death rates), which need not respond to the same factors, at least not in the same way. Thus, merging the variance in these rates into a single, compound parameter may blurry the signal of any effects they carry.

Evidence for a relationship between population dynamic parameters was ambiguous: strength of density dependence and intrinsic growth rate tended to increase together, but the spread of data was high and statistical significance was marginal, perhaps because sample size was relatively small. On possible interpretation for this result is that fast-growing populations also tend to experience crowding faster and, thus, stronger density dependence (Wang *et al.* 2013). For instance, resource shortage may constrain intrinsic growth rate, thus alleviating crowding and reducing density dependence. Alternatively, higher intrinsic growth rate may favour poorer competitors that are more strongly affected by density (MacArthur & Wilson 1967; Mueller 2009; Reznick 2014). Clarifying the nature of this relationship will require either experimental or genetic data. Nonetheless, this relationship in light of our structural equation model because it suggests that intrinsic growth rate may affect mean density indirectly rather than directly, through an effect on strength of density dependence. This contradicts the expectation of simple, direct effects from standard population models (Eq. 1). While many studies have assessed the relationship between r and K (Luckinbill 1978; Bell 1990; Kuno 1991; Hendriks *et al.* 2005; Underwood 2007; Fitzsimmons *et al.* 2010; Jasmin & Zeyl 2012), few have directly addressed that between r and α. Yet, these parameters were also found to increase together across experimental aphid populations (Agrawal *et al.* 2004), across *Drosophila* populations experimentally subject to divergent selection (Mueller 2009), and across natural guppy populations with divergent life histories (Reznick, Bryant & Bashey 2002), suggesting that this might be a common pattern.

We note that our estimates refer to intra-annual dynamics; results may differ between years, as well as for interannual dynamics. Further, our data account for adults only because species identification of immatures is currently impractical for most oribatid mites (Norton &

Behan-Pelletier 2009). Even when identification is feasible, extraction efficiency from soil samples may differ between immatures and adults, e.g. immatures may be more prone to desiccation or occur in a microhabitat different from that of adults (Andre *et al.* 2002). The extent to which population dynamics of adults is representative of that of immatures (or of the population as a whole) depends on how much their densities correlate through time, and this has been shown to vary among oribatid mite species (Stamou & Sgardelis 1989). Thus, our results should be viewed with this limitation in mind. However, the effect of competition is often stronger in juvenile stages (White 2008). Thus, omission of immatures is more likely to under- than overestimate density dependence and its effects.

This study provided evidence that the landscape distribution of the soil mite *R. ovulum* is shaped by a combination of direct effects of density-dependence, body size and habitat. Further, populations with higher intrinsic growth rates tended to experience stronger density dependence, although statistical support for this association was less clear. Our results point to density dependence rather than intrinsic growth rate as a key determinant of species distribution. However, they suggest that intrinsic growth rate may indirectly affect density, contrary to what one would expect from standard population models. Further, we show that population dynamic parameters may not capture all relevant effects on density, as exemplified by those of body size and habitat. Thus, standard population models appear to provide poor representations of heterogeneous species distributions unless important phenotypic and environmental covariates are also taken into account.

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Authors’ contributions

PACLP, EF, RAN and JWM conceived and designed the study. PACLP performed data sampling and analysis. PACLP, F, RAN and JWM wrote the manuscript.

Data accessibility

All data used in this paper will be archived in the Dryad Digital Repository upon acceptance.

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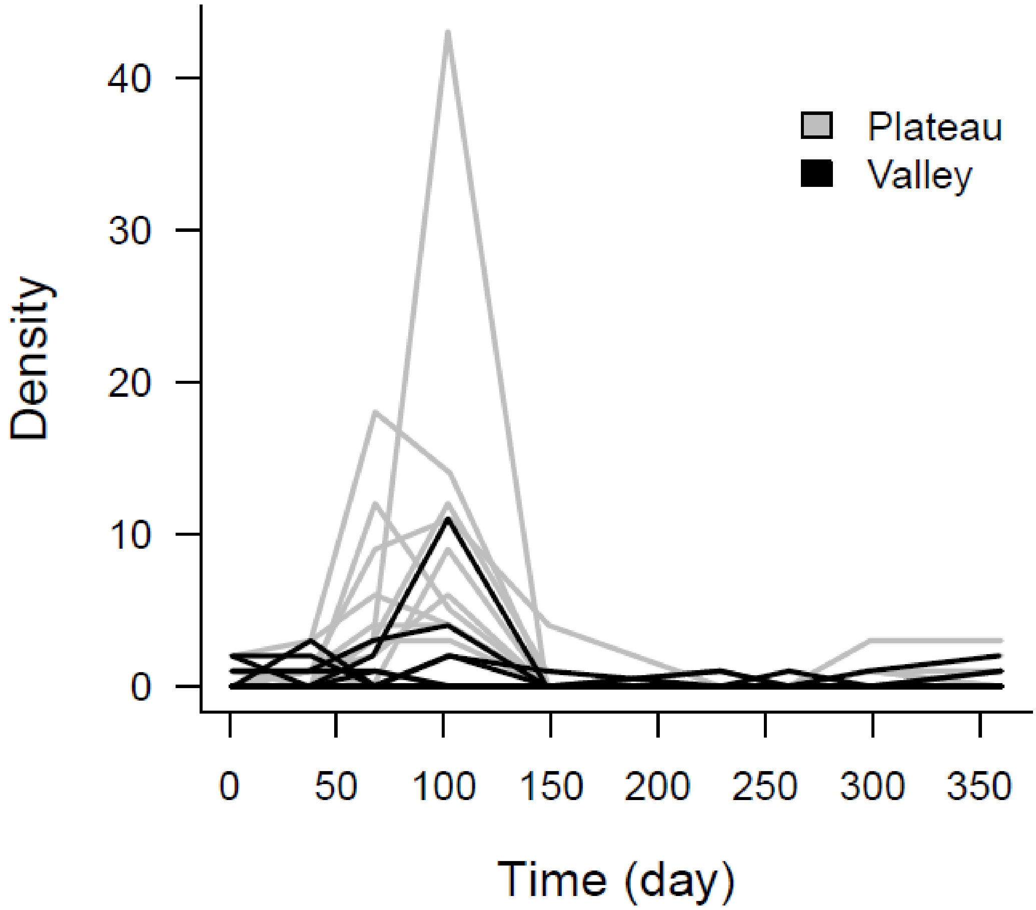

Figure 1. Density fluctuations of populations of the soil mite *Rostrozetes ovulum* throughout the study, counting from the first sampling day. Vertices indicate sampling events (n = 9), and lines connect consecutive densities of the same population (n = 17).

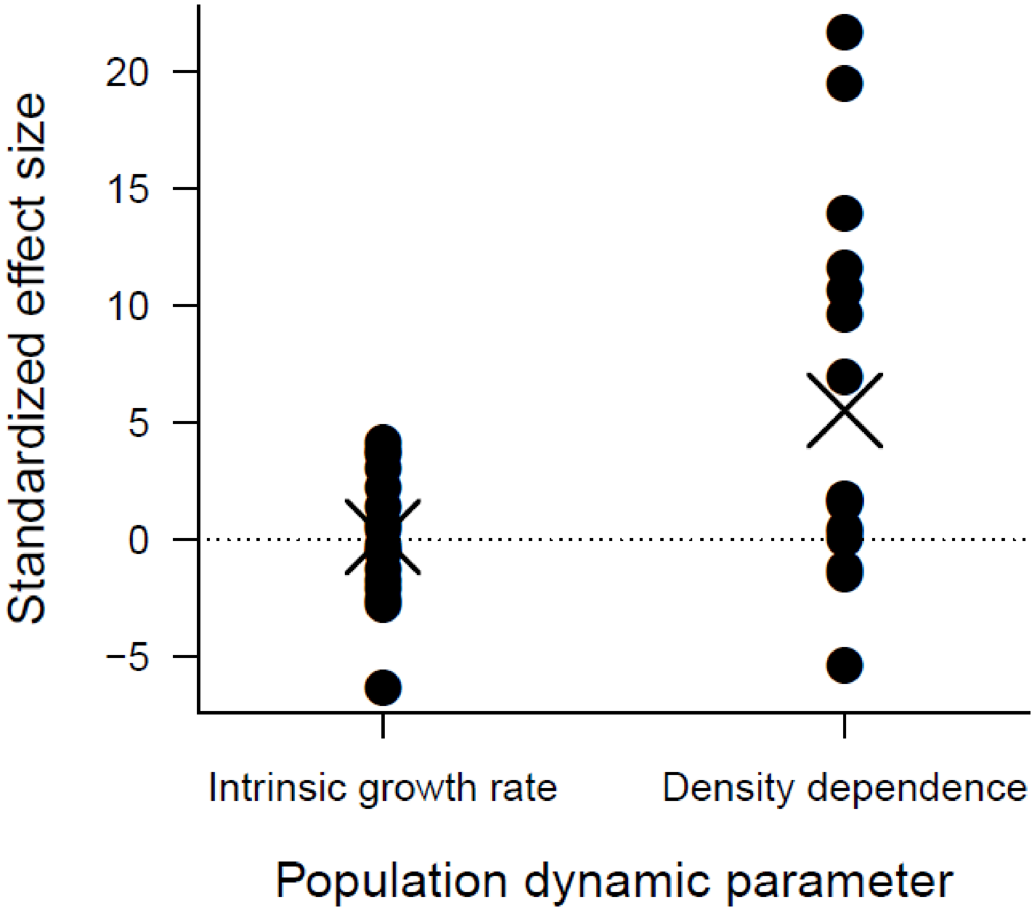

Figure 2. Standardized effect sizes of population dynamic parameters of the soil mite *Rostrozetes ovulum*. Each point represents a population (n = 17 for each parameter). The dotted line marks the null expectation (i.e. zero). The “×” indicates the observed mean.

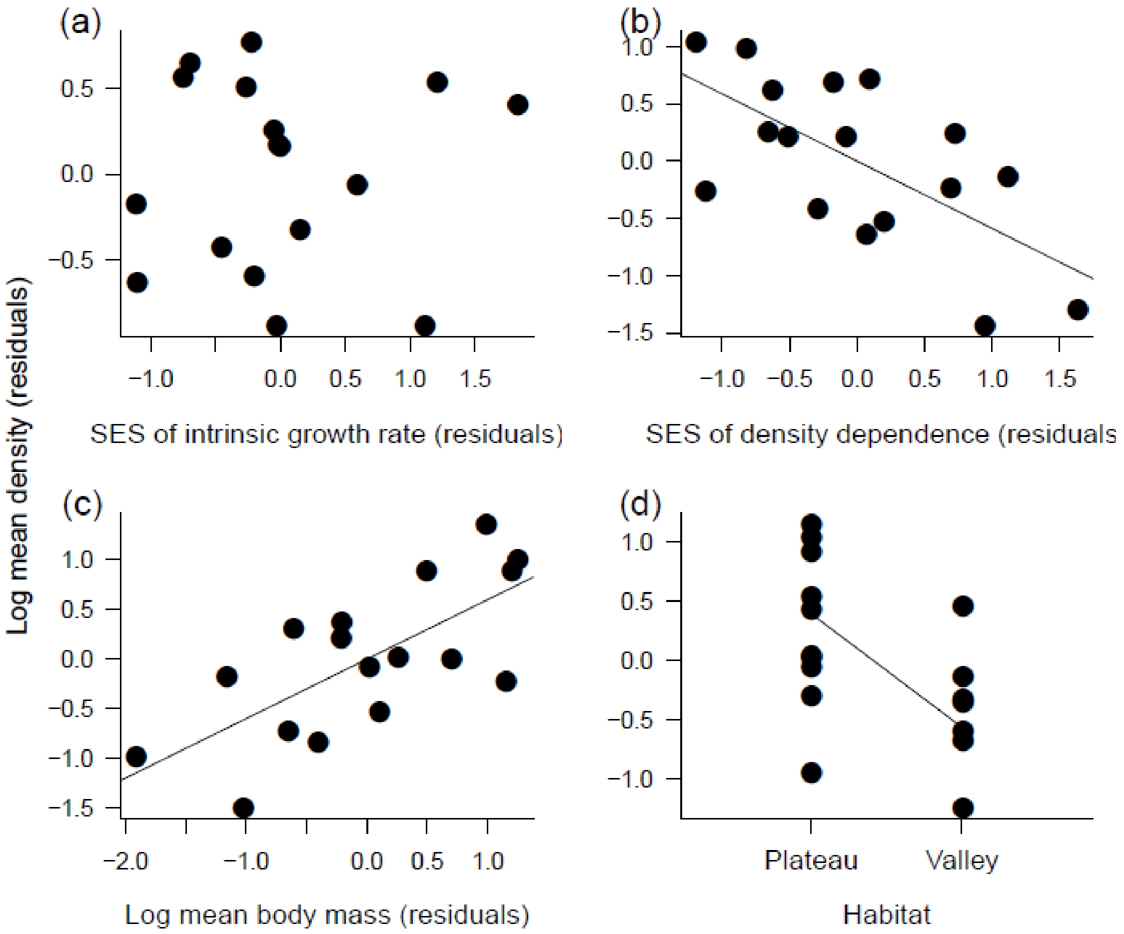

Figure 3. Partial regressions of mean density of the soil mite *Rostrozetes ovulum* on (a) intrinsic growth rate, (b) strength of density dependence, (c) mean adult body mass and (d) habitat. Mean density and mean adult body mass were analyzed in log scale; intrinsic growth rate and density dependence were analyzed as standardized effect sizes (SES) to account for bias in their estimation. Points represent populations (n = 17 in each plot), and lines represent significant regression fits.

Figure 4. Structural equation model of hypothesized relationships among population dynamics, individual phenotype and environment in the soil mite *Rostrozetes ovulum* (n = 17). Black, red and gray arrows indicate positive, negative and non-significant unidirectional effects, respectively; arrow thickness is proportional to the magnitude of standardized regression coefficients. Intrinsic growth rate and density dependence were analyzed as standardized effect sizes obtained through null modelling. Mean density and mean adult body mass were log-transformed. Habitat was coded as a dummy variable, and its coefficient indicates change in the response variable from plateaus to valleys.

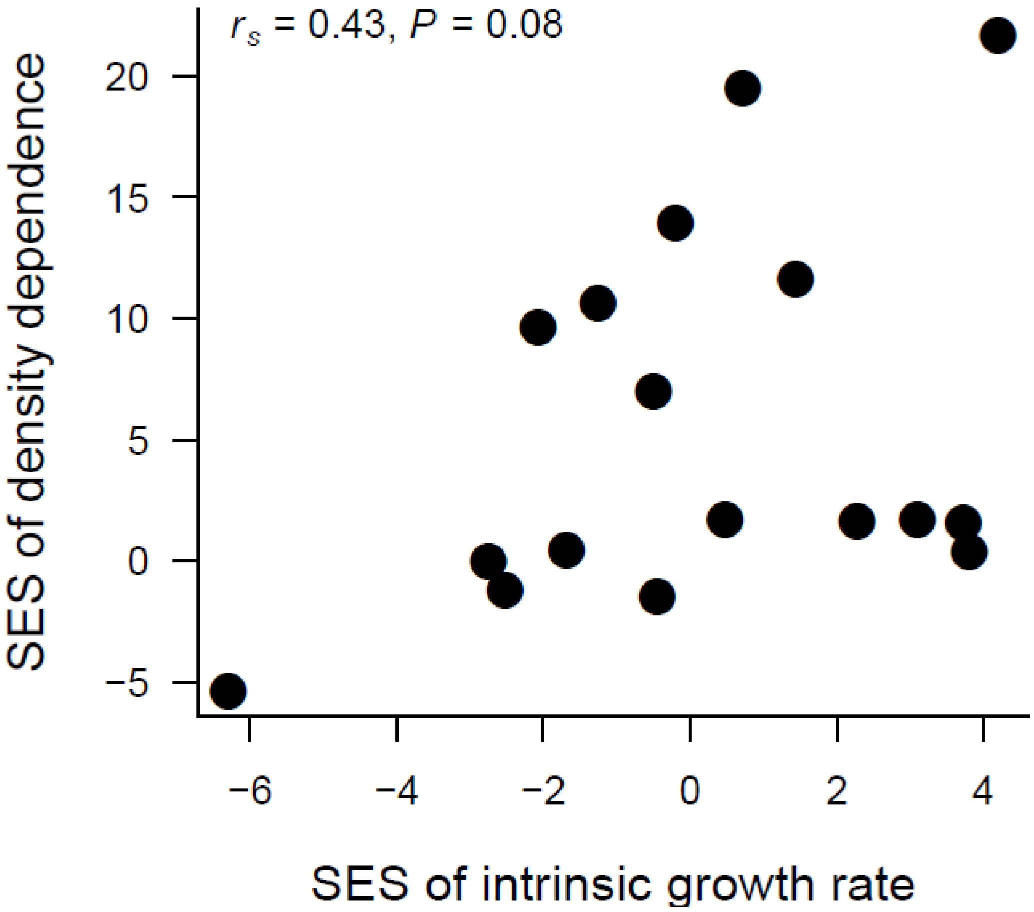

Figure 5. Relationship between standardized effect sizes (SES) of strength of density dependence and intrinsic growth in the soil mite *Rostrozetes ovulum*. Statistical significance was assessed with Spearman's rank correlation (r_s). Points represent populations (n = 17).

CAPÍTULO 3

Habitat submersion risk drives intraspecific shift in seasonal temperature-size response

Pequeno, P. A. C. L. P.; Franklin, E.; Norton, R. A.; Morais, J. W.

Em revisão em *Biology Letters*

Abstract

In most ectotherms, adult body size decreases with warming, the so-called "temperature-size rule" (TSR). The oxygen hypothesis attributes this phenomenon to higher thermal sensitivity of oxygen demand relative to supply, and predicts that TSR should be stronger in aquatic vs. terrestrial habitats. However, empirical tests have been limited to comparative analyses, largely of temperate species. Here, we show that the adult body mass of the cosmopolitan soil mite *Rostrozetes ovulum* declined as maximum temperature increased over seasons in an Amazonian rainforest. Further, percent decline per ºC was almost four-fold higher in riparian forests subject to short-term flooding than in non-riparian forests that never flood. Our results provide unique evidence that the oxygen hypothesis could also explain intraspecific shifts in TSR, and show that temperature-driven plasticity can be important even in the climatically-buffered soils of tropical rainforests.

Key words: Amazonia, climate change, life history, metabolic rate, phenotypic plasticity, wetland

Background

Ectotherms typically grow smaller with warming – the so-called “temperature-size rule” (TSR) –, but a unifying explanation for TSR has been elusive [1]. Recently, it has been suggested that TSR is an adaptation to safeguard aerobic scope under higher oxygen demand [1–4]. As temperature increases, metabolic rate increases much faster than the rate of oxygen diffusion through body fluids [1,5]. Because larger organisms have a smaller surface area for gas exchange relative to their volume, they should face stronger respiratory constraints, thus favouring the evolution of a plastic size reduction with warming [1].

This “oxygen hypothesis” uniquely predicts that TSR should be stronger in aquatic habitats than in terrestrial ones, given the much lower diffusion rate of oxygen in water relative to air. Indeed, laboratory, latitudinal and seasonal TSR are stronger in aquatic relative to terrestrial species [2–4,6]. Yet, whether the oxygen hypothesis also applies within species is unknown. Moreover, almost all data on seasonal TSR come from temperate regions [4,6,7]. Although thermal amplitude is lower in the tropics, overall temperatures are higher, and even short-term temperature extremes can significantly impact ectotherm development and adult size [8].

Many soil invertebrates occur simultaneously in terrestrial and semiaquatic habitats [9]. *Rostrozetes ovulum* (Berlese, 1908) (Acari: Oribatida) is one such species: this parthenogenetic mite occurs from dry uplands to swampy forests and floodplains worldwide [10]. In central Amazonia, *R. ovulum* adults can survive submersion for months, as well as produce eggs under water [11]. Development from egg to adult takes around six weeks [11], and adult abundance peaks yearly for two to three months [10,11], suggesting a life cycle of four to five months. As adults occur year-long, development must occur at different seasons.

In this study, we collected *R. ovulum* adults over a year from habitats in central Amazonia differing markedly in submersion risk: riparian forest, which is subject to waterlogging and temporary floods during heavy rains, and non-riparian forest, which never floods. We predicted that (1) adult body size should decrease as ambient temperature increases throughout the year, but (2) the magnitude of this decrease should be stronger in riparian, flood-prone forest.

Methods

Field work was carried out in a primary forest remnant (800 ha) in Manaus, Brazilian Amazonia (03°04’34”S; 59°57’30”W). Annual rainfall is relatively high (2200 mm), and mean monthly air temperature typically varies in the range 24 – 27 ºC [12]. The landscape comprises an alternation between dry uplands and moist valleys. In the latter, water table depth decreases from ca. 0.8 to 0.1 m as the rainier season proceeds, causing soils to waterlog permanently for weeks [13]. Meanwhile, heavy rains cause valleys to flood for hours to a few days [13,14].

We sampled 20 transects located across the study site, each being 20 m long and at least 150 m away from any other (supplementary material, table S1). Half of the transects were located along drainage catchments (riparian forest), and half on uplands at least 150 m away from any stream (non-riparian forest). Transects were sampled on eight occasions over a year (June, July, August and November 2014; and January, March, April and June 2015). In each transect, one soil sample was extracted each meter with an aluminum soil corer (3.5 × 3.5 × 5 cm). Soil samples were taken to laboratory, where soil animals were extracted into 95 percent alcohol using a Berlese-Tullgren apparatus [10]. *R. ovulum* adults were sorted and photographed under a microscope to measure their body length (L) and width (W) (μm). Then, body mass (M) was estimated as $\log M = -17.17 + 3.00 \log (L + W)$ [15].

Daily temperature readings were obtained online from the nearest station of the Brazilian Institute for Meteorology, 10 km away from the study site (supplementary material, table S2). Monthly means of air and soil temperature (5 cm deep) correlate well in central Amazonia (*r* = 0.82, n = 18) [16]. Moreover, spatial variance in soil temperature is negligible in central Amazonian forests, with the difference in hourly measurements of soil temperature between uplands and valleys being ca. 0.5 ºC [17]. This justifies our use of data on nearby air temperature as a proxy for local soil temperature seasonality. We considered mean and maximum daily temperature readings for each day of 2014 and 2015. The maximum was used because short-term extreme temperatures can have disproportionate effects on development [8], and is also more variable than the mean in the region [16].

We used generalized linear mixed modelling (GLMM) to model body mass (µg) as a Gamma-distributed dependent variable, assuming a log link. Transect was used as a random factor, to control for potential non-independence among individuals from the same transect. We considered five *a priori* combinations of predictors representing alternative hypotheses on the drivers of body mass: (1) intercept-only model (i.e. no predictors); (2) habitat as single predictor; (3) temperature as single predictor; (4) temperature and habitat as independent effects; and (5) an interaction between temperature and habitat. Models including temperature were expanded in two ways. First, we built separate models for mean and maximum temperature. Second, we considered different time windows for the effect of temperature on adult body mass. Because *R. ovulum* takes about two months to develop from egg to adult, current adult body mass should reflect temperatures experienced during some two-month interval up to five months before sampling (i.e. the estimated lifespan of *R. ovulum* in the field). Thus, temperature variables were computed for time intervals of 0 – 60, 30 – 90, 60 – 120 and 90 – 150 days before sampling, and separate models were built for each.

All models were ranked according to Akaike's Information Criterion corrected for sample size (AICc), and models with a difference of two units or less relative to the model with lowest AICc were favoured. Model explanatory power was assessed as the squared correlation between observed and predicted values (R^2), and mean percent change in body mass per ºC was calculated as ($exp^{(\text{slope})} - 1) \times 100$ [2]. All analyzes were performed in R 3.3.2 [18].

Results

A single model was clearly supported over the alternatives: body mass decreased with increasing daily maximum temperature between 0 and 60 days before sampling, with average reduction in body mass being higher in riparian than in non-riparian forest (Table 1, Fig. 1). For each 1 ºC increase in maximum temperature, average body mass decreased by 9.72% in non-riparian forest, but by 38.85% in riparian forest. Therefore, average body mass declined 1.4-fold over the observed temperature gradient in non-riparian forest, but 3.27-fold in riparian forest.

Discussion

The oxygen hypothesis predicts stronger TSR in aquatic vs. terrestrial habitats due to low oxygen diffusion rates in water, which should limit the viability of larger bodies with high metabolic costs [1–4,6]. Our results on the soil mite *R. ovulum* support this idea: adult body mass decreased over the year with increasing maximum temperature during the time frame of the mite's development, and percent decrease per ºC was almost fourfold higher in riparian forests subject to short-term flooding than in non-riparian forests which never flood.

Wetlands cover about one third of the Amazon basin, and near Manaus they cover as much as 40% of the landscape [14]. In the same region, species of mites, collembolans, millipedes and ground-dwelling beetles are known to occur simultaneously in dry and flood-prone habitats [9]. Contrary to *R. ovulum*, most such species endure submersion as eggs [9], but even then adult mass can be affected by temperature thorough changes in egg mass [5].

Thus, the habitat-driven TSR found here might be a common adaptation of Amazonian soil fauna.

More generally, our results advance our understanding of TSR in two ways. First, the oxygen hypothesis has been tested (and supported) at the species level, by comparing TSR between terrestrial and aquatic organisms [2–4,6]. Our study provides unique evidence that the same mechanism could also explain intraspecific variation in seasonal TSR. Second, almost all data on seasonal TSR come from mid-latitudes [4,6,7]. Here we show that TSR can be important even in tropical rainforests, were climate seasonality is relatively mild. Other important biological processes are known to be driven by ambient temperature in Amazonian rainforests, e.g. soil respiration rate [19].

There was much unexplained variance in our data (i.e. $R^2 = 0.20$). This is to be expected, as we used nearby air temperature as a proxy for the actual soil temperature experienced by *R. ovulum*. Thus, any effect of maximum air temperature on adult mass must have been indirect. Further dilutions in this effect can be expected due to variability in other drivers of body size (e.g. resource availability) [4,6,7] and a relatively low number of generations within years [4], as appears to be the case of *R. ovulum*. Lastly, our study is correlative, and our results should be viewed with this caveat in mind. Nonetheless, it is clear that the oxygen hypothesis correctly predicted the between-habitat shift in the mite's seasonal TSR; it is unclear why this should be so if the hypothesis does not hold.

The higher seasonal plasticity of body size in riparian relative to non-riparian forests suggests that the landscape heterogeneity of tropical forests promotes adaptive divergence between sympatric populations of soil animals. Climate warming may thus be expected to have widespread effects on soil fauna, both between and within species.

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Authors' contributions

PACLP, EF, RAN and JWM conceived the study. PACLP collected and analyzed the data. All authors contributed to the manuscript.

Data accessibility

The datasets supporting the conclusions of this article will made available in a public database upon acceptance.

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Competing interests

The authors declare that they have no competing interests.

Ethical statement

This study complied with local legal requirements; no special licence was required for this kind of research.

Table 1. Top five generalized linear mixed models of seasonal variation in *Rostrozetes ovulum*'s body mass (n = 116), ranked according to Akaike's Information Criterion corrected for sample size (AICc). Numbers in bold indicate well supported models (ΔAICc < 2).

Model equation	R^2	ΔAICc
$exp(13.61 - 0.25T_{max,60} - 8.44habitat + 0.23T_{max,60}habitat)$	0.20	**0.00**
$exp(7.37 - 0.15T_{max,60} - 0.13habitat)$	0.14	6.39
$exp(7.75 - 0.16T_{max,60})$	0.12	6.61
$exp(16.99 - 0.54T_{mean,90} - 11.49habitat + 0.41T_{mean,90}habitat)$	0.16	7.28
$exp(22.09 - 0.72T_{mean,60} - 13.26habitat + 0.47T_{mean,60}habitat)$	0.14	9.95

Note: Models assumed Gamma-distributed errors and log link, with transect as random factor to control for autocorrelation among individuals sampled from the same transect. $T_{max,60}$: maximum daily temperature between 0 and 60 days prior to sampling; $T_{mean,60}$, $T_{mean,90}$: mean daily temperature between 0 and 60 days, and between 30 and 90 days prior to sampling, respectively; *habitat*: habitat (riparian or nor-riparian forest, the former used as baseline).

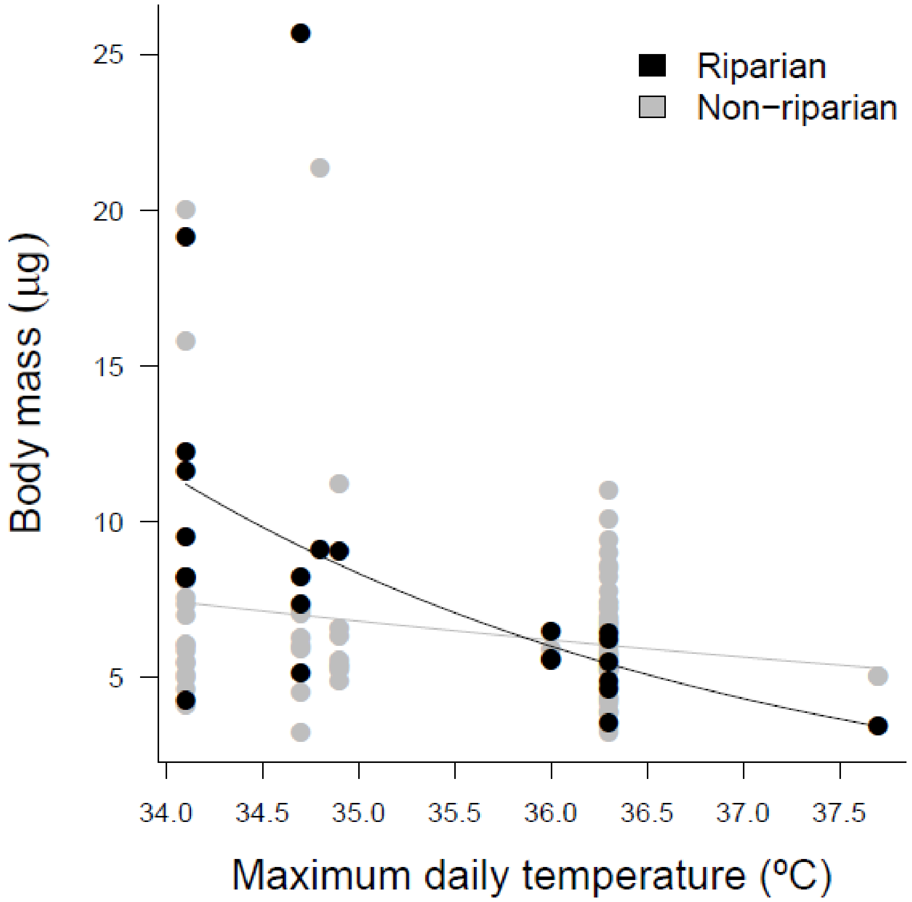

Figure 1. Seasonal temperature-size response of *Rostrozetes ovulum* in a central Amazonian rainforest. Points represent individuals (n = 116); lines represent the fittest model (see Table 1). Maximum daily temperature refers to the period between 0 and 60 days prior to sampling.

CAPÍTULO 4

Sympatric morphophysiological divergence in a widespread soil parthenogen

Pequeno, P. A. C. L. P.; Franklin, E.; Norton, R. A.; Morais, J. W.

Submetido para *Journal of Evolutionary Biology*

Abstract

There remains considerable uncertainty about the pace of adaptive evolution, particularly at local spatial extents. In soils, hundreds of species can coexist per square meter, many of which are asexual. This suggests that their diversification may have depended more on opportunities for adaptation than on reproductive barriers. Here, we investigated whether the submersion risk to which soil organisms are commonly exposed can drive sympatric divergence in submersion tolerance and its putative morphological correlates in the widespread parthenogenetic oribatid mite, *Rostrozetes ovulum*. We sampled adults from many sites across an Amazonian rainforest landscape (800 ha), distributed between flood-prone valleys and dry uplands. We found that submersion survival time had a bimodal distribution that was unrelated to habitat. Nonetheless, discriminating between component distributions with mixture modelling revealed that, among longer-lived mites, those from valleys survived submersion two weeks longer than those from uplands, on average. Further, valley mites tended to have a higher density of cuticular rugosities (pits and grooves) and, to a lesser degree, to be more slender and smaller. Yet, submersion tolerance and morphology were unrelated after accounting for habitat, suggesting the habitat submersion risk drives divergence in the former, but not the latter. Lastly, mites farther apart were no more different than expected by chance, suggesting that dispersal is not limiting so that between-habitat phenotypic divergence is maintained by ongoing plasticity and/or selection. These findings highlight the potential for sympatric ecological divergence in soil invertebrates, which might help explain the exceptionally high biodiversity of soils.

Key words: divergent selection, local adaptation, mosaic sympatry, Oribatida, plastron respiration, soil invertebrate

Introduction

Adaptive evolution reflects a balance between diversifying and homogenizing forces. On the one hand, divergent selection can create locally adapted populations and, eventually, drive reproductive isolation (i.e. speciation) (Darwin & Wallace, 1858; Nosil, 2012; Langerhans & Riesch, 2013; Shafer & Wolf, 2013). On the other hand, migration (i.e. exchange of individuals between populations) and sexual reproduction (i.e. exchange of genes between individuals) tend to have the opposite effect, by mixing the genetic composition of populations (Futuyma, 2010; Gorelick & Heng, 2011). The balance between these forces is mediated by the dispersal pattern of organisms relative to the scale of environmental heterogeneity (Garant *et al*., 2007; Mallet *et al.*, 2009; Baythavong, 2011), as well as by phenotypic plasticity, which is itself an evolvable trait (Thibert-Plante & Hendry 2011; Nonaka *et al*., 2015; Chevin & Hoffmann, 2017). This complex suite of conditions has rendered the general pace of contemporary adaptive evolution rather uncertain: is it typically "sluggish" (Futuyma, 2010) or "easy" (Mallet, 2008)?

Much of Earth's biodiversity dwells in soils, where hundreds of invertebrate species commonly co-occur in a few grams of substrate (Wardle, 2006). Yet, the evolutionary origins of this diversity remain largely unknown. The small body size typical of soil invertebrates limits their active dispersal while simultaneously increasing the chance of passive dispersal, so that dispersal limitation is uncommon even over spatial extents of several kilometers (Costa *et al.*, 2013). This suggests that evolutionary divergence among soil invertebrate populations may be hampered by migration at local spatial extents. Curiously, though, soils harbour an unusually high number of asexual species (Scheu & Drossel, 2007; Fontaneto & Barraclough, 2015), which by definition cannot evolve reproductive isolation. Actually, recent evidence suggests that asexuality can facilitate speciation, possibly due to absence of the homogenizing effect of recombination and amphimixis on the genome (Tang *et al.*, 2014).

Such findings suggest that the diversification of soil parthenogens may have largely depended on opportunities for adaptation and, more generally, that divergent selection may be strong enough in soils to foster evolutionary differentiation at relatively small spatial extents (Adis & Junk, 2002; von Saltzwedel *et al.*, 2014).

Soil organisms are commonly challenged by waterlogging and flooding (Villani *et al.*, 1999). Generally, soil fauna abundance decreases as flood disturbance increases across habitats, but many species – variously termed "generalist", "euryoecious", "tolerant" or "opportunist" – persist under such conditions (Adis & Junk, 2002; Marx *et al.*, 2012; Coyle *et al.*, 2017). Submersion tolerance is a plastic trait which often relies on anaerobic metabolism (Schmitz & Harrison, 2004). Accordingly, gradual submersion can significantly enhance survival under anoxia (Zerm & Adis, 2003). In parallel, irregular body surfaces support thin air layers (i.e. plastrons) which allow aerial respiration under water (Marx & Messner, 2012). This could be enhanced by having a smaller or more slender body, as the distance between body surfaces and internal tissues would be reduced, thus facilitating gas diffusion (Villani *et al.*, 1999; Tufová & Tuf, 2005). Indeed, arthropods often grow smaller under hypoxia (Harrison *et al.*, 2010). Thus, non-isolated populations exposed to contrasting submersion regimes may diverge in physiology and morphology, either due to a plastic response to contrasting habitats, selection on genetically-fixed traits and/or norms of reaction, or a combination thereof. Asexuality may facilitate this pattern because parthenogens dispense with the indirect sperm transfer typically employed by sexual soil animals, and thus may colonize flood-prone habitats more easily (Beck, 1969; Norton & Palmer, 1991).

We examined these issues using the parthenogenetic oribatid mite *Rostrozetes ovulum* (Berlese, 1908). This is a cosmopolitan species particularly abundant in tropical forests (Pequeno *et al.*, 2017). As most soil arthropods, *R. ovulum* feeds on dead plant matter (Illig *et al.*, 2005), is rather small (300 – 400 µm long) and has little mobility. Development from egg to adult takes around six weeks (Beck, 1969), and adult abundance peaks yearly for two to three months (Beck, 1969; Pequeno *et al*., 2017), suggesting a life cycle of four to five months. As reproduction is not perfectly synchronous (Beck, 1969), there may be several, partially overlapping generations per year.

In central Amazonia, Franklin *et al*. (2001) found that *R. ovulum* adults from two floodplain sites survived experimental submersion three to fivefold longer than adults from two non-flooded forest sites, on average. However, while floodplains are flooded by great rivers, most non-flooded or *terra firme* forests are traversed by numerous valleys with hydromorphic soils. In such habitats, water table depth decreases from ca. 0.8 to 0.1 m over the rainier season, causing permanent waterlogging for weeks and short-term floods (hours to a few days) during or after heavy rains (Hodnett *et al.*, 1997; Junk *et al.*, 2011). Pequeno *et al*. (2017) found that *R. ovulum*'s abundance decreased from uplands to valleys and from drier to rainier months in central Amazonia, suggesting that submersion risk may drive phenotypic divergence between valleys and uplands, e.g. in submersion tolerance. In *R. ovulum*, the cuticle contains numerous pits (i.e. foveolae) sometimes connected by grooves, as well as a thick waxy layer known as cerotegument. Apparently, such structures are fixed in adults and assist in the formation and tenacity of a plastron, which has connection to the tracheal system (Messner *et al.*, 1992). Thus, they may relate to submersion tolerance.

We hypothesized that habitat submersion risk drives morphophysiological divergence in *R. ovulum* in the absence of dispersal limitation. In an Amazonian rainforest landscape (800 ha), we sampled living *R. ovulum* adults from many sites distributed between uplands and valleys. Then, we experimentally determined individual submersion tolerance, and assessed putative morphological correlates. We predicted that (1) individuals from valleys would survive submersion longer than individuals from uplands (2) morphology would differ consistently between uplands and valleys, with the latter dominated by more slender, smaller individuals covered by more surface irregularities (i.e. pits and grooves); (3) variation in submersion survival time would relate independently to morphological traits and to habitat (e.g. due to differentiation in anaerobic metabolic rate); (4) dispersal would not be limiting, so that there would be no relationship between phenotypic and geographic distance among individuals.

Materials and methods

Field work

The study was performed in a large forest remnant (800 ha) in Manaus, Brazilian Amazon (03°04'34"S; 59°57'30"W). Annual rainfall is 2200 mm and mean monthly air temperature usually ranges between 24 and 27 ºC, with a drier, warmer season (monthly rainfall below 100 mm) from July to September (Pequeno *et al.*, 2017). Altitude varies between *ca.* 40 and 90 m asl. Soils change from clayish in uplands to sandy-hydromophic in valleys. In the latter, the water table begins to rise around April, and reaches its shallowest depth around June, when soils waterlog (Hodnett *et al.*, 1997).

In April 2016 (i.e. right before the beginning of prolonged soil waterlogging), we sampled 17 sites spread all over the study area, each at least 150 m away from any other. Seven sites were located in valleys (drained either by temporary or permanent streams), while remaining transects were located in uplands at least 150 m away from any stream. The distance among transects varied from 156 to 2989 m, averaging 1204 ± 653 m (mean ± SD). In each site, we recorded geographic coordinates, and randomly harvested litter and superficial soil (down to 5 cm deep) over a 20 m-long transect until filling 30 L of a plastic bag. This material was taken to laboratory, where soil animals were extracted into neutral water using Berlese-Tullgren apparatus (Franklin & Morais, 2006). Extracted animals were surveyed for living and undamaged *R. ovulum* adults under a stereomicroscope. This yielded 85 mites, which were transferred to individual experimental units to determine submersion tolerance.

Submersion experiment

Submersion survival time was determined by subjecting collected specimens to experimental submersion in water (Pequeno & Franklin, 2014). Each experimental unit consisted of a plastic pot (4 cm tall, 2.5 cm wide) with a 2.5 cm-thick layer of plaster of Paris as substrate. One oat flake was added to feed the mite *ad libitum* throughout the experiment. In each pot, a single mite was introduced and completely submerged with sterilized, neutral water to a depth of 0.5 cm. Experimental units were kept in a BOD chamber (12 hours with light at 27 ºC, and 12 hours without light at 21 ºC), and were monitored at alternate days until mite death. Mites were suspected dead if unresponsive to tactile stimuli; in such cases, they were further monitored for 2 weeks to confirm death. However, in most cases, death could be unambiguously determined by the spread of legs. Throughout the experiment, experimental units were cleaned from growing algae, and water was replaced whenever it became turbid (ca. once a week). Some individuals disappeared during the experiment, probably by hiding within larger pores formed during preparation of the substrate. Thus, submersion survival time (days) could be determined for 59 of the 85 tested individuals. Dead specimens were preserved in 95% ethanol.

Morphological measurements

All specimens recovered from the submersion experiment had their dorsal surfaces micrographed under an environmental scanning electron microscope (Quanta 250, FEI Company, USA). Micrographs were used to quantify several morphological traits (Fig. 1).

Only micrographs of individuals for which all traits of interest could be unambiguously determined were used (n = 42). First, body length (*L*) and width (*W*) were measured to estimate two further traits, body volume and shape. Volume was estimated as $V = 4/3\pi r^3$, where $r = 0.201(L + W)$ (Caruso & Migliorini, 2009). Shape was estimated as the length-to-width ratio, so that an increasing ratio represented change from a more rounded body to a more slender one. Second, the estimated the proportion of the dorsum covered by grooves connecting foveolae; when present, grooves always spread from the posterior to the anterior part of the dorsum, forming a diffuse network (Fig. 1). Measuring grooves directly was impractical, so we coded "groove cover" as an ordinal variable: (1) grooves absent; (2) groves covering 0 – 33% of the dorsum; (3) groves covering 33 – 66% of the dorsum; and (4) grooves covering 66 – 100% of the dorsum. Third, a 50 × 50 µm quadrat was delimited over the top of the mite's dorsal surface, at the intersection between the longitudinal and transversal axes of the body. Within this area, foveolar density (i.e. number of foveolae lying within the quadrat by more than a half) and mean foveolar diameter (i.e. average of four random foveolae within the quadrat) were determined.

Data analysis

All analyses were performed in R 3.3.2 (R Core Development Team, 2016), with aid of packages "MASS", "diptest", "mixtools" and "MuMIn". To test for differences in submersion survival time between habitats, we employed Generalized Linear Modelling (GLM) assuming Gamma-distributed errors and log link, a standard setting for continuous, positive-valued variables. However, prior to analysis, we observed that submersion survival time had a seemingly bimodal distribution (Fig. 2). This was supported by a direct test of the null hypothesis of unimodality (Silverman's test, $P = 0.034$), suggesting the occurrence of two, statistically distinct subpopulations (Ahmed & Walther, 2012). Contrary to our expectation, though, bimodality was not related to habitat: uplands and valleys had exactly the same mean survival time, i.e. 42 days (GLM: $t = 0.009$, $P = 0.99$), suggesting that bimodality was caused by some other, unidentified factor. Thus, we used mixture modelling to identify the component distributions, classify individuals according to them and analyze each separately. We used function gammamixEM() from the "mixtools" package to fit a Gamma mixture model to survival time assuming either a single distribution or two mixed distributions, and compared them with Akaike's Information Criterion. As expected, the mixture model was much better than the single-distribution one (ΔAIC = 30.53), and split individuals into long-lived (i.e. surviving over three weeks; n = 39) and short-lived ones (i.e. surviving less than three weeks; n = 20) (Fig. 2). Accordingly, we used GLM to test for the effect of habitat on survival time within each group.

To visualize morphological space, we reduced the dimensionality of morphological data (n = 42) to two dimensions with Principal Component Analysis (PCA). Variables were standardized to zero mean and unit variance to give them equal weight in the ordination. To test for differences in morphology (i.e. PCA axes) between habitats (upland or valley), we used Multivariate Analysis of Variance (MANOVA).

To assess the independent contributions of habitat and morphology to submersion tolerance, we also used GLMs. As before, this was performed for the two survival time groups separately. Pairing of all variables reduced the sample size in each group (n = 24 for long-lived individuals, and n = 17 for short-lived individuals). We used AIC corrected for small sample size (AICc) to determine the most parsimonious combination of predictors of survival time up to two, to keep a reasonable number of degrees o freedom given the small sample sizes. Models distant up to two AICc units of the model with lowest AICc were judged well supported; among these, those with fewer parameters were favoured to avoid spurious inference (Arnold, 2010).

Lastly, we examined the extent to which phenotypic differentiation reflected geographic distance among sampling sites, e.g. due to easier migration among closer sites. To this aim, we created three matrices of Euclidian distances among individuals (n = 41): a phenotypic matrix (based on all morphological traits plus submersion survival time, all standardized to zero mean and unit variance), an environmental matrix (based on habitat, coded as a dummy variable), and a geographic matrix (based on the geographic coordinates of sampling sites). We tested for the effects of environmental and geographic distances on phenotypic distance while controlling for each other using partial Mantel tests (999 permutations). We also assessed the relationship between environmental and geographic distances with a Mantel test.

Results

Submersion tolerance varied widely among individuals, with survival time ranging between 1 and 111 days and averaging 42 days. Survival time differed between habitats among long-lived individuals (GLM: $t = 2.40$, $P = 0.02$, n = 39), but not among short-lived individuals (GLM: $t = 0.31$, $P = 0.75$, n = 20) (Fig. 3). In the former case, individuals from valleys survived submersion two weeks longer than those from uplands, on average (i.e. 71 vs. 56 days, respectively).

Morphological traits were collinear, so that the first and second PCA axes accounted for 61 and 19% of the variance in the data, respectively. Along the main morphological gradient (i.e. increasing scores of first PCA axis), individuals tended to be larger, more rounded, to have fewer but larger foveolae, and to have a smaller proportion of the dorsum covered by grooves (Table 1, Fig. 4). Cuticular traits, particularly groove cover, correlated more strongly to the main morphological gradient than did size or shape (Table 1).

Morphology segregated clearly between valleys and uplands, so that habitat accounted for 41% of the variance in PCA scores (MANOVA: Wilk's $\lambda = 0.59$, $F = 13.81$, $P = 0.00003$, n = 42). Namely, the grooved, more slender morphology tended to occur in valleys, whereas the groove-less, more rounded morphology tended to occur in uplands (Fig. 5).

Model selection using AICc confirmed that submersion survival time could only be predicted among long-lived individuals (Table 2). However, survival time was not clearly related to any of the measured morphological traits. Rather, habitat consistently entered top-ranked models; as before, valley individuals survived two weeks longer than upland ones, on average (Table 2). Other supported models either explained less variance or contained more parameters (Table 2).

Lastly, and in line with previous results, phenotypic and environmental distances were positively correlated independently of geographic distance ($r = 0.26$, $P = 0.001$), but the latter had no effect on phenotypic distance while controlling for the environment ($r = -0.09$, $P = 0.91$). Also, environmental and geographic distances were unrelated ($r = 0.003$, $P = 0.375$).

Discussion

Adaptive evolution is a complex function of many factors, and there remains substantial uncertainty about its pace, particularly under ongoing gene flow. Soil invertebrates provide a useful system for exploring this issue: being small-bodied, they are expected to respond to local environmental heterogeneity. Moreover, many soil animal species are parthenogenetic, suggesting that ecological opportunities for adaptation rather than reproductive barriers have played a major role in their diversification. Here, we provide evidence that, in a central Amazonian rainforest landscape, adults of the parthenogenetic soil mite *Rostrozetes ovulum* from flood-prone valleys can survive submersion considerably longer than do those from dry uplands. Further, *R. ovulum*'s morphology tends to differ between such habitats, particularly regarding cuticular traits. This differentiation is independent of geographic distance, which had no effect on its own. Such results support the hypothesis that the studied populations are undergoing phenotypic differentiation despite no dispersal limitation, at least partly because of habitat submersion risk. Yet, as submersion tolerance was unrelated to morphology after accounting for habitat, factors other than submersion risk are probably also involved.

Unexpectedly, *R. ovulum*'s submersion survival time had a bimodal distribution. This contrasts with the unimodal distribution determined experimentally for *R. ovulum* adults from an Amazonian floodplain (albeit at a smaller spatial extent) (Pequeno & Franklin, 2014), and was not related to variation between habitats. This pattern suggests overlap of distinct statistical subpopulations (Ahmed & Walther, 2012). For instance, we may have inadvertently sampled two *R. ovulum* generations, so that some individuals were senescent and succumbed early in the experiment (i.e. the short-lived group). Alternatively, if previous submersion increases submersion tolerance (Zerm & Adis, 2003), then longer-lived individuals may have experienced natural submersion prior to the experiment. Whatever the cause of bimodality, it conditioned the expression of submersion tolerance, so that between-habitat difference in survival time was only evident among longer-lived mites.

Morphology also diverged between habitats, with valley mites having more surface irregularities (i.e. higher density of smaller foveolae, higher proportion of dorsum covered by interfoveolar grooves) compared to upland mites. To a lower extent, valley mites also tended to be more slender and smaller than upland mites. Such features are expected to facilitate plastron formation and retention under water (Messner *et al.*, 1992), as well as gas diffusion through respiratory entrances and internal tissues by reducing the distance between them (Villani *et al.*, 1999; Tufová & Tuf, 2005). However, there was no clear relationship between survival time and morphological traits while accounting for habitat. We notice that splitting the data according to the bimodal distribution of survival time decreased sample size in each group and thus, reducing the power to detect any such relationship within each group. Nonetheless, this result suggests that *R. ovulum*'s submersion tolerance depended on factors other than morphology, e.g. anaerobic metabolic rate. This contradicts our expectation that morphological divergence between habitats would result from divergence in submersion risk. As the best described function of cerotegument structures in mites and other soil arthropods is anti-wetting and plastron formation (Wolff *et al*., 2017), this result suggests that such structures might have some other, unidentified function.

At the spatial extent we studied, environmental and geographic distances were independent, and the latter had no effect on phenotypic distance. This is consistent with the idea that, despite the limited active dispersal of soil invertebrates, dispersal is not limiting over spatial extents of several kilometres due to passive dispersal (Costa *et al.*, 2013). This suggests that the mechanism creating the observed between-habitat divergence is robust to ongoing migration. Recent theory predicts that, in non-isolated populations in heterogeneous landscapes, the evolutionary basis of phenotypic differentiation depends on the timing of expression of phenotypic plasticity throughout the life cycle. If plasticity is expressed before dispersal, locally adapted genotypes tend to be favoured, as dispersers cannot adjust to different habitats and are selected against (Thibert-Plante & Hendry, 2010). In contrast, if plasticity is expressed after dispersal, dispersers can adjust to new conditions, and plastic generalist genotypes are favoured (Thibert-Plante & Hendry, 2010), especially if dispersers cannot choose habitats adaptively (Nonaka *et al*., 2015). If so, the expected degree of plasticity may still differ between habitats, but is harder to predict, depending on a number of parameters and assumptions (Baythavong, 2011; Lande, 2015; Chevin & Hoffmann, 2017).

In this light, we hypothesize that variation in *R. ovulum*'s submersion tolerance is mainly the expression of relatively few, "general purpose genotypes", assuming submersion tolerance is a plastic trait and adults are the dispersive stage but do not select their habitat adaptively due to passive dispersal. Thus, between-habitat difference in submersion tolerance would mainly reflect a plastic response to contrasting submersion regimes, either elicited locally, throughout development, and/or during the arrival of dispersers. In addition, several studies have found the degree of plasticity to increase with environmental variability across populations of both animals and plants (Chevin & Hoffmann, 2017). Thus, it is also possible that higher submersion tolerance in valley mites among longer-lived individuals reflects adaptive divergence in reaction norms, as valleys are more variable regarding soil submersion than uplands (Hodnett *et al.*, 1997). In contrast to submersion tolerance, cuticular traits are seemingly fixed once individuals become adults, suggesting that between-habitat differentiation in adult morphology is more likely to reflect local adaptation in response to some unidentified selective agent(s).

One important caveat of this study is that we could not determine experimentally the genetic basis of between-habitat phenotypic differentiation. Rearing the studied species in laboratory under non-submerged conditions resulted in unexpectedly high mortality. Likewise, obtaining individual DNA sequences from the mite proved rather difficult. Nonetheless, habitat-related genetic variation at local spatial extents has been shown for another oribatid parthenogen (von Saltzwedel *et al.*, 2014), and there is evidence for significant heritability of morphological, physiological and life history traits across diverse asexual species (Browne *et al.*, 2002; Carter *et al.*, 2012; Messiaen *et al.*, 2012; Tully & Potapov, 2015). Thus, the investigated traits probably have standing genetic variation.

In conclusion, this study provides evidence of between-habitat divergence in submersion tolerance and morphology at local spatial extents in a widespread soil parthenogen, the oribatid mite *R. ovulum*. This divergence occurs despite no evidence for dispersal limitation, suggesting it is maintained by ongoing processes, either phenotypic plasticity, selection, or a combination thereof. Plasticity is more likely to account for habitat differentiation in submersion tolerance, as this trait is plastic during the dispersive stage (i.e. adults), and habitat differ markedly in submersion risk. Conversely, the measured morphological are fixed in adults and, thus, cannot be adjusted to non-natal habitats. Therefore, the “grooved” and “non-grooved” morphologies are more likely to be local adaptations to valleys and uplands, respectively. Yet, because submersion tolerance and morphology were unrelated, morphological adaptations are unlikely to reflect habitat submersion risk, suggesting the involvement of some unknown selective agent. Overall, this study highlights the potential for sympatric ecological divergence in soil invertebrates, particularly in the absence of sex, which might help explain the exceptionally high biodiversity of soils.

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Table 1. Summary of Principal Component Analysis (PCA) of morphological traits of the soil mite *Rostrozetes ovulum* (n = 42). r_{PC1} and r_{PC2} are the correlations between traits and the first and second PCA axes, respectively.

Morphological trait	mean	min	max	r_{PC1}	r_{PC2}
Body volume ($\times 10^6$ µm^3)	5.96	3.48	10.02	0.38	0.64
Body length-width ratio	1.64	1.48	1.82	-0.42	-0.50
Foveolar density (# per 2500 µm^2)	35.53	31	49	-0.46	0.23
Mean foveolar diameter (µm)	5.24	3.57	6.58	0.46	-0.41
Groove cover (ordinal)	1.52	1	4	-0.49	0.30

Table 2. Top ranked generalized linear models of submersion survival time in relation to morphological traits and habitat in the soil mite *Rostrozetes ovulum*. Survival time was modelled as a Gamma-distributed response related to predictors with a log link. Analysis was performed separately for long-lived (n = 24) and short-lived individuals (n = 17), as classified by a Gamma mixture model (see main text). Bold numbers indicate supported models (ΔAICc < 2). *habitat*: binary variable (0 = upland, 1 = valley); *ratio*: body length-width ratio; *grooves*: proportion of dorsum covered by grooves, ordinal variable; *diameter*: mean foveolar diameter; *density*: foveolar density.

Group	Rank	Survival time equation	R^2	ΔAICc
Long-lived	1	$\exp(4.06 + 0.31\times \mathit{habitat})$	0.20	**0.00**
	2	$\exp(5.19 - 0.37\times \mathit{diameter})$	0.17	**1.08**
	3	$\exp(1.79 + 0.29\times \mathit{habitat} + 1.49\times \mathit{ratio})$	0.25	**1.34**
	4	$\exp(4.07 + 0.43\times \mathit{habitat} - 0.18\times \mathit{grooves})$	0.23	**1.91**
	5	$\exp(4.60 + 0.22\times \mathit{habitat} - 0.18\times \mathit{diameter})$	0.23	2.12
Short-lived	1	$\exp(1.84)$	0.00	**0.00**
	2	$\exp(0.41 + 0.50\times \mathit{diameter})$	0.05	1.88
	3	$\exp(1.70 + 0.24\times \mathit{habitat})$	0.01	2.71
	4	$\exp(1.90 - 0.20\times \mathit{grooves})$	0.01	2.81
	5	$\exp(2.36 - 0.01\times \mathit{density})$	0.01	2.83

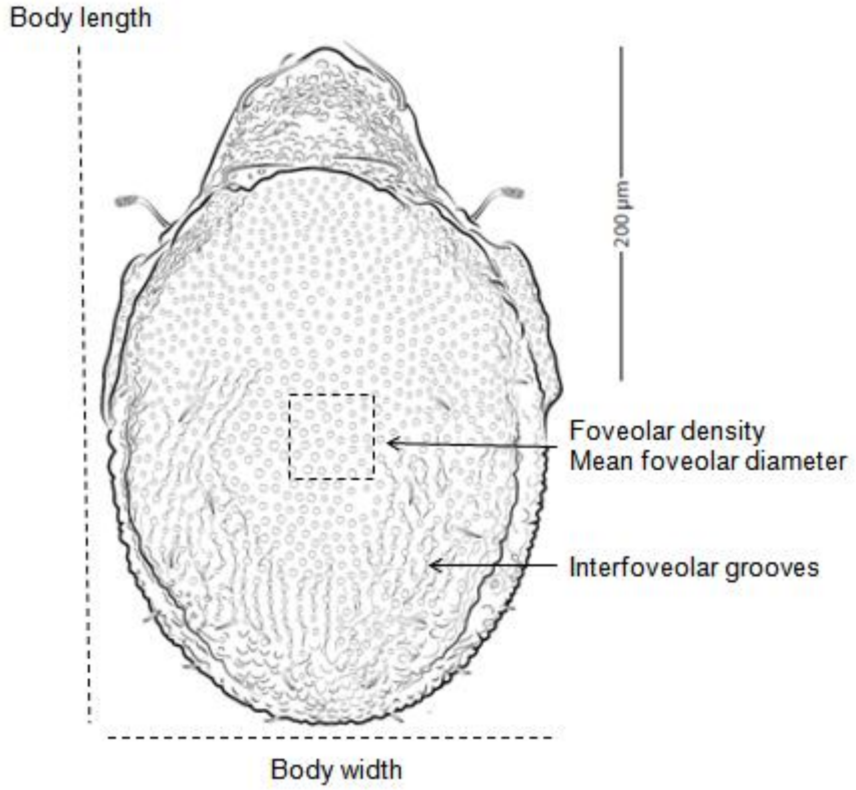

Figure 1. Schematic representation of an adult specimen of the soil mite *Rostrozetes ovulum*, with measured morphological traits indicated (dorsal view). Foveolar density and mean foveolar diameter were assessed within the highlighted quadrat (50 × 50 µm). Illustration by E. Franklin.

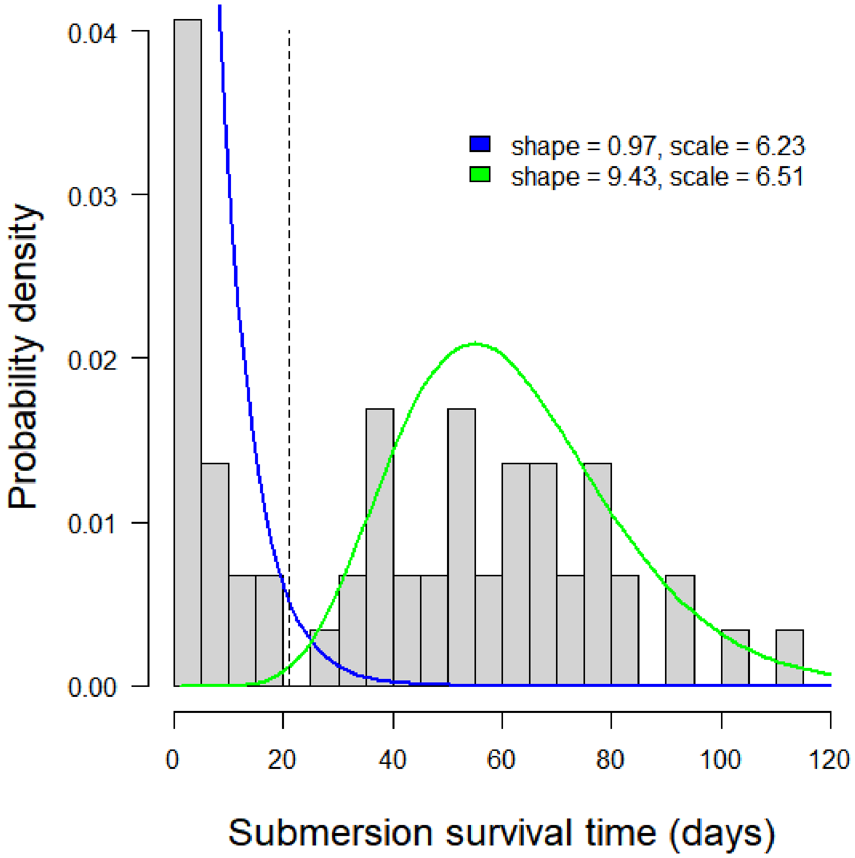

Figure 2. Probability distribution of submersion survival time of the soil mite *Rostrozetes ovulum* (n = 59). Survival times were determined experimentally from adult individuals collected across an Amazonian rainforest landscape (800 ha). Curves represent component distributions of the fitted Gamma mixture model. The dashed line represents the separation between long-lived and short-lived individuals (i.e. surviving more or less than three weeks, respectively), as classified by the model.

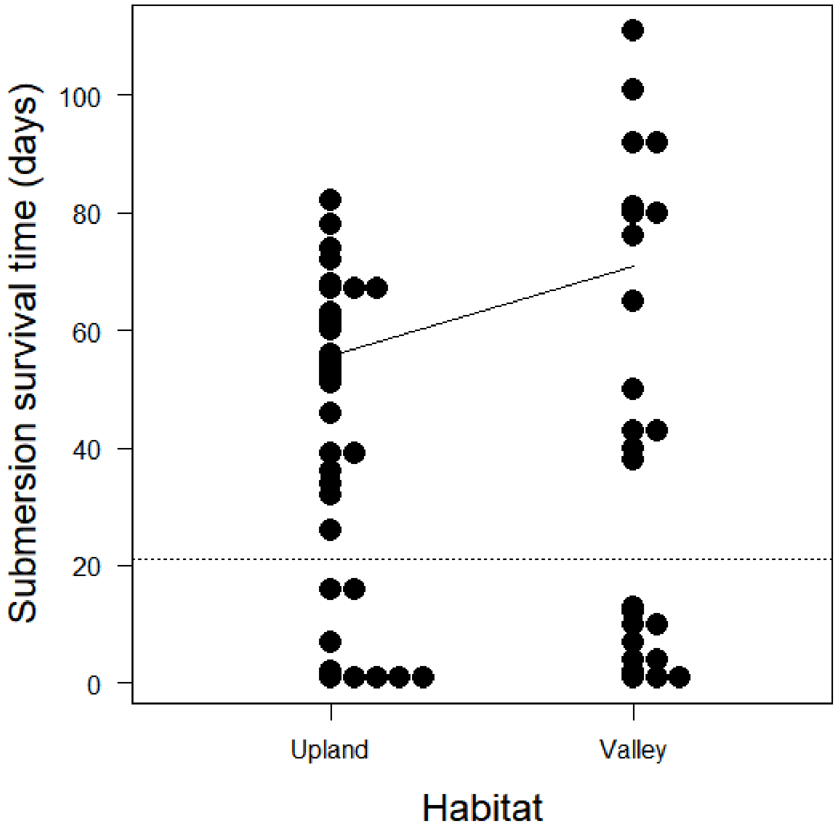

Figure 3. Relationship between submersion survival time and habitat in the soil mite *Rostrozetes ovulum*. Each point represents an adult individual collected across an Amazonian rainforest landscape (800 ha). The dotted line separates individuals belonging to the long-lived (i.e. surviving over three weeks, n = 39) and short-lived groups (i.e. surviving shorter than three weeks, n = 20), as classified by the fitted Gamma mixture model. The solid line represents the significant fit of a Generalized Linear Model (Gamma-distributed errors, log link) to the long-lived group.

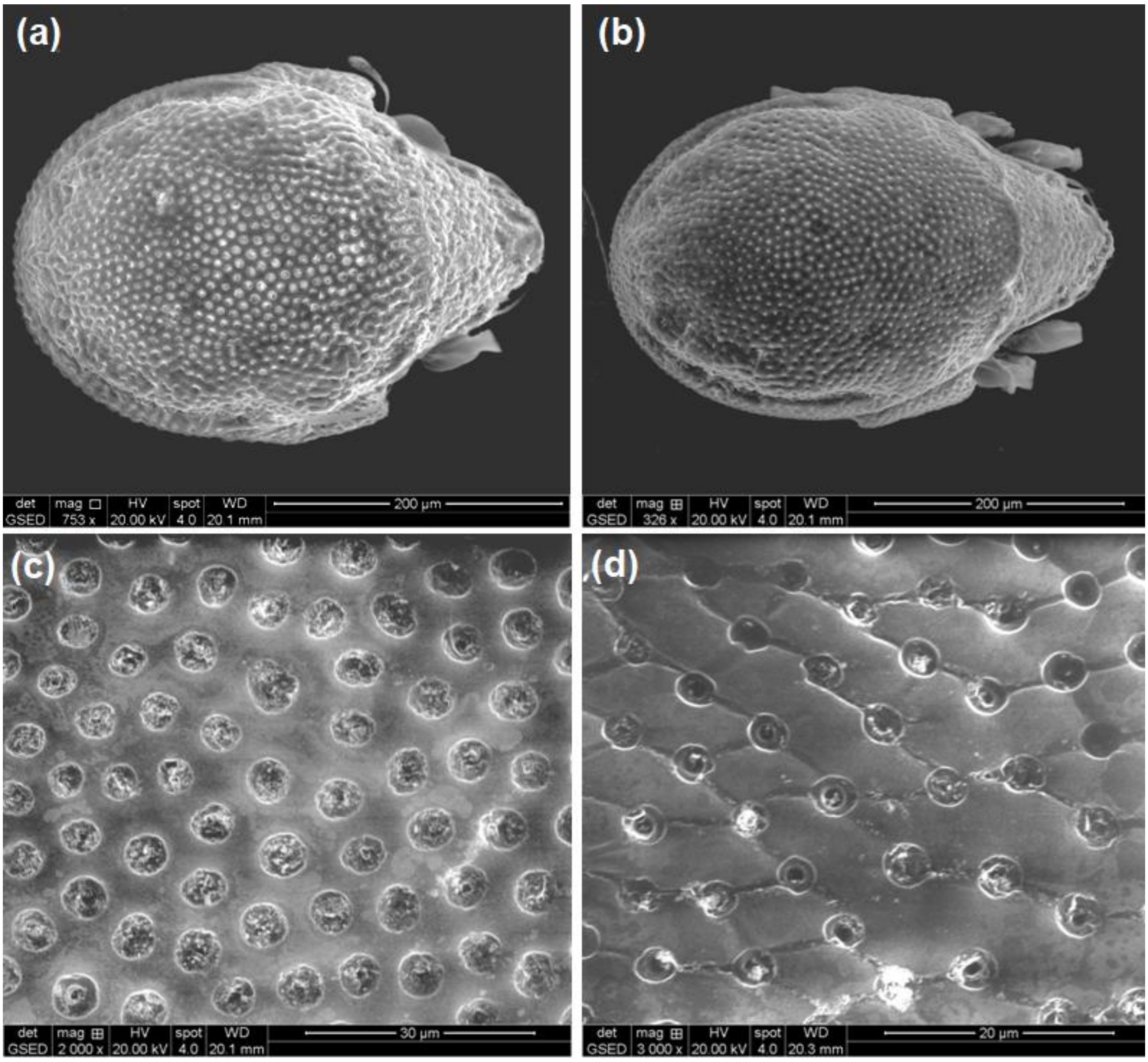

Figure 4. Morphological variation of the soil mite *Rostrozetes ovulum* in an Amazonian rainforest landscape (800 ha). (a) and (b): dorsal view of representative specimens from uplands and valleys, respectively; (c) and (d): close view of dorsal cuticle without and with interfoveolar grooves, respectively. All images were obtained with environmental scanning electron microscopy.

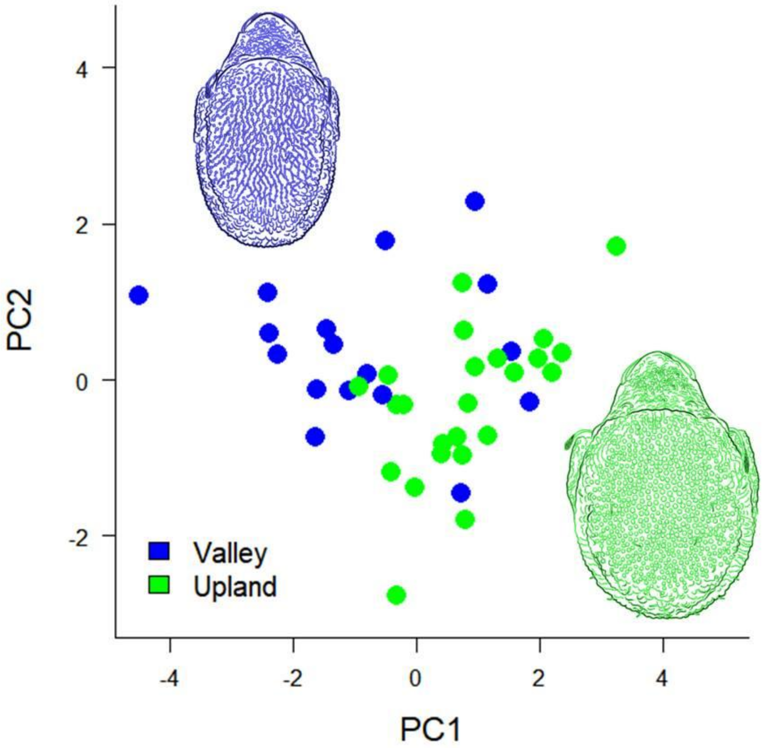

Figure 5. Relationship between morphology and habitat in the soil mite *Rostrozetes ovulum*, as represented by the first two dimensions of Principal Component Analysis (PCA). Each point represents an adult individual (n = 42) collected across an Amazonian rainforest landscape (800 ha). Five morphological traits were summarized: body volume, body length:width ratio, foveolar density, mean foveolar diameter and proportion of dorsum covered by grooves. Representative morphologies are shown for valleys (top left) and uplands (bottom right). Illustrations by E. Franklin.

SÍNTESE

Nesta tese, revelamos que a variação entre platôs e baixios na Amazônia central afeta tanto a dinâmica quanto a composição de populações simpátricas de um artrópode edáfico representativo, o ácaro *Rostrozetes ovulum* (Figura 1). A densidade média de *R. ovulum* diminui dos platôs para os baixios, e esta tendência foi independente do efeito da denso-dependência e do tamanho corporal médio (Figura 1). Como a denso-dependência mede a intensidade da competição intrapopulacional, este resultado sugere que a diferença de densidade entre hábitats não tem a ver com disponibilidade de recursos. Paralelamente, o tamanho corporal é um preditor bem estabelecido da taxa reprodutiva em artrópodes, sugerindo que a diferença entre hábitats também não está relacionada a diferenças de história de vida entre populações. A causa mais provável para a diferença de densidade entre hábitats seria uma diferença na taxa de mortalidade extrínseca, e.g. devido ao risco de alagamento, como previsto pela tese.

O tamanho corporal fornece um elo entre a variação fenotípica entre indivíduos e a dinâmica populacional de *R. ovulum*: populações com indivíduos maiores tenderam a atingir densidades maiores, independentemente de outros fatores (Figura 1). Entretanto, o tamanho corporal médio não diferiu entre hábitats; ao invés disto, o grau de plasticidade fenotípica do tamanho diferiu: a variação sazonal do tamanho foi substancialmente maior nos baixios que nos platôs (Figura 1), consistente com a hipótese de que a sazonalidade do tamanho reflete adaptação à limitação do oxigênio em solos alagáveis. Isto sugere que, no caso do tamanho corporal, o habitat tem selecionado mais fortemente entre normas de reação (i.e. grau de plasticidade do tamanho) que entre tamanhos geneticamente fixados.

As diferenças morfo-fisiológicas entre hábitats sugerem um cenário mais complexo de divergência fenotípica. Os maiores tempos de sobrevivência à submersão foram observados em indivíduos de baixio (Figura 1), consistente com uma resposta direta ao risco de alagamento. Além disso, indivíduos provenientes de baixios tiveram mais irregularidades cuticulares que indivíduos de platôs (Figura 1). Em menor grau, indivíduos de baixios também tenderam a ser mais ovais e menores que aqueles de platôs. No entanto, não houve relação entre tolerância à submersão e morfologia. Assim, a diferenciação morfologia entre hábitats não parece estar relacionada ao risco de submersão do hábitat, mas assim a algum outro fator não considerado. Além disso, a divergência fenotípica entre hábitats foi independente da distância geográfica entre populações, a qual não teve qualquer efeito sobre a diferenciação fenotípica. Isto sugere que, na extensão espacial estudada, dispersão não é um fator limitante e, portanto, a divergência entre hábitats provavelmente é mantida por processos atualmente em curso, como plasticidade fenotípica (mais provável no caso da tolerância à submersão) ou seleção contra migrantes (mais provável no caso da morfologia) (ver cap. 4).

Em geral, a evidência apresentada suporta a divergência fenotípica entre populações de *R. ovulum* habitando platôs e baixios, ao menos em parte causada pelo risco de submersão. Determinar a base genética desta divergência seria um próximo passo natural desta investigação. Por outro lado, é interessante notar que a força da denso-dependência (i.e. competição intraespecífica) explicou parte da variação na densidade populacional média, e não teve relação com o hábitat (Figura 1). Assim, tanto mortalidade extrínseca (i.e. risco de submersão) quanto recursos parecem ser importantes na organização espacial das populações de *R. ovulum*, atuando de forma independente. Identificar quais recursos e como eles afetam as populações seria outra extensão natural deste estudo. Por exemplo, talvez a diferença morfológica entre hábitats, a qual não esteve relacionada à tolerância à submersão, tenha alguma relação com disponibilidade diferencial de recursos entre hábitats (e.g. teores de nutrientes limitantes como C, N e P).

Além disto, houve alguma evidência de que a força da denso-dependência – um dos limitantes da densidade populacional – tendeu a aumentar com a taxa intrínseca de crescimento. Por sua vez, a taxa intrínseca de crescimento foi algo maior nos platôs que nos baixios. Isto levanta a hipótese de que o hábitat tenha efeitos antagônicos sobre a densidade. Se, por um lado, a densidade diminui dos platôs para os baxios independentemente de outros fatores, uma taxa intrínseca de crescimento maior nos platôs levaria a uma denso-dependência mais forte neste ambiente e, consequentemente, a uma densidade menor (Figura 1). Entretanto, a causalidade da relação (e a direção do efeito) entre taxa intrínseca de crescimento e força da denso-dependência não está clara (Figura 1). Estas questões têm implicações ecológicas gerais (e.g. teoria de seleção *r*-*K*), e seria interessante examiná-las com mais detalhe.

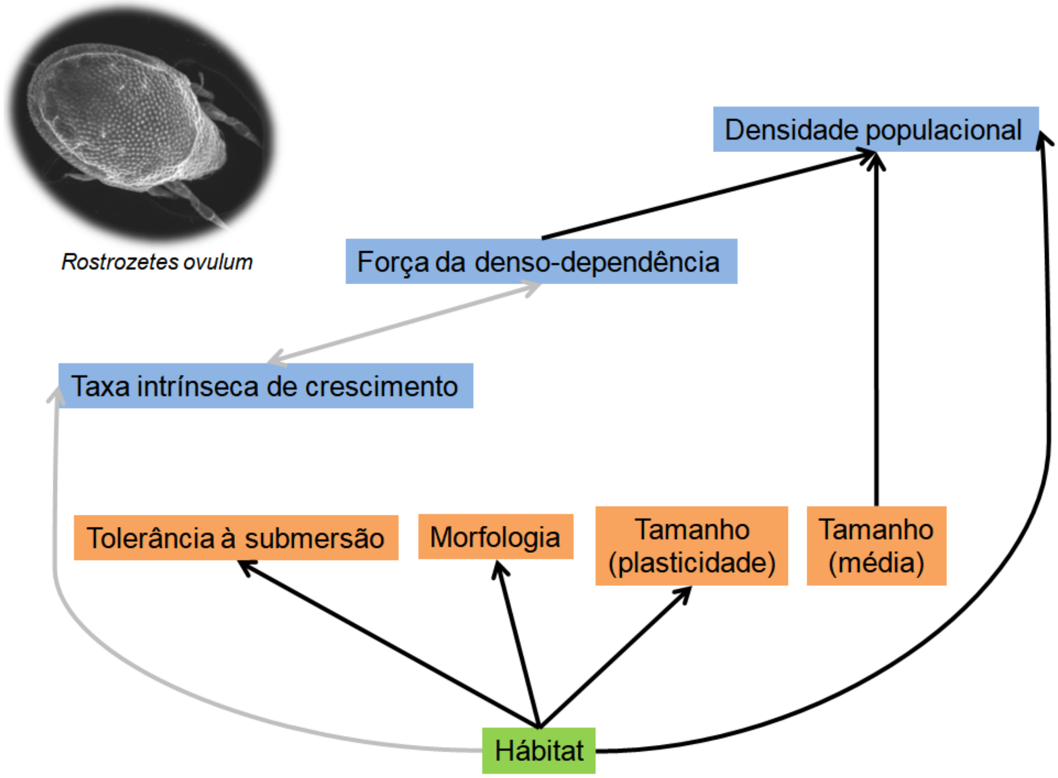

Figura 1. Síntese das relações investigadas nesta tese. As caixas representam variáveis, agrupadas em três categorias: ambiente (verde), fenótipo (laranja) e dinâmica populacional (azul). Setas unidirecionais representam relações causais; setas bidirecionais representam correlações de natureza indefinida. Setas pretas indicam relações estatisticamente significativas; setas cinzas representam relações marginalmente significativas.

De modo geral, nossos resultados ressaltam a importância da consideração simultânea de fatores espaciais e temporais na compreensão de fenômenos ecológicos e evolutivos, e indicam divergência fenotípica em extensões espaciais relativamente pequenas – dentro de um fragmento florestal urbano –, e na ausência de reprodução sexuada. Propomos que a "simpatria de mosaico" pode ser um modo comum de diferenciação da fauna do solo, especialmente em populações clonais como as de *R. ovulum*. Ao que tudo indica, ecologia e evolução são duas faces da mesma moeda, como anteviram Darwin, Wallace, Haeckel e seus contemporâneos. A vida pode estar se diversificando em todo lugar, o tempo todo – bem debaixo do nosso nariz.

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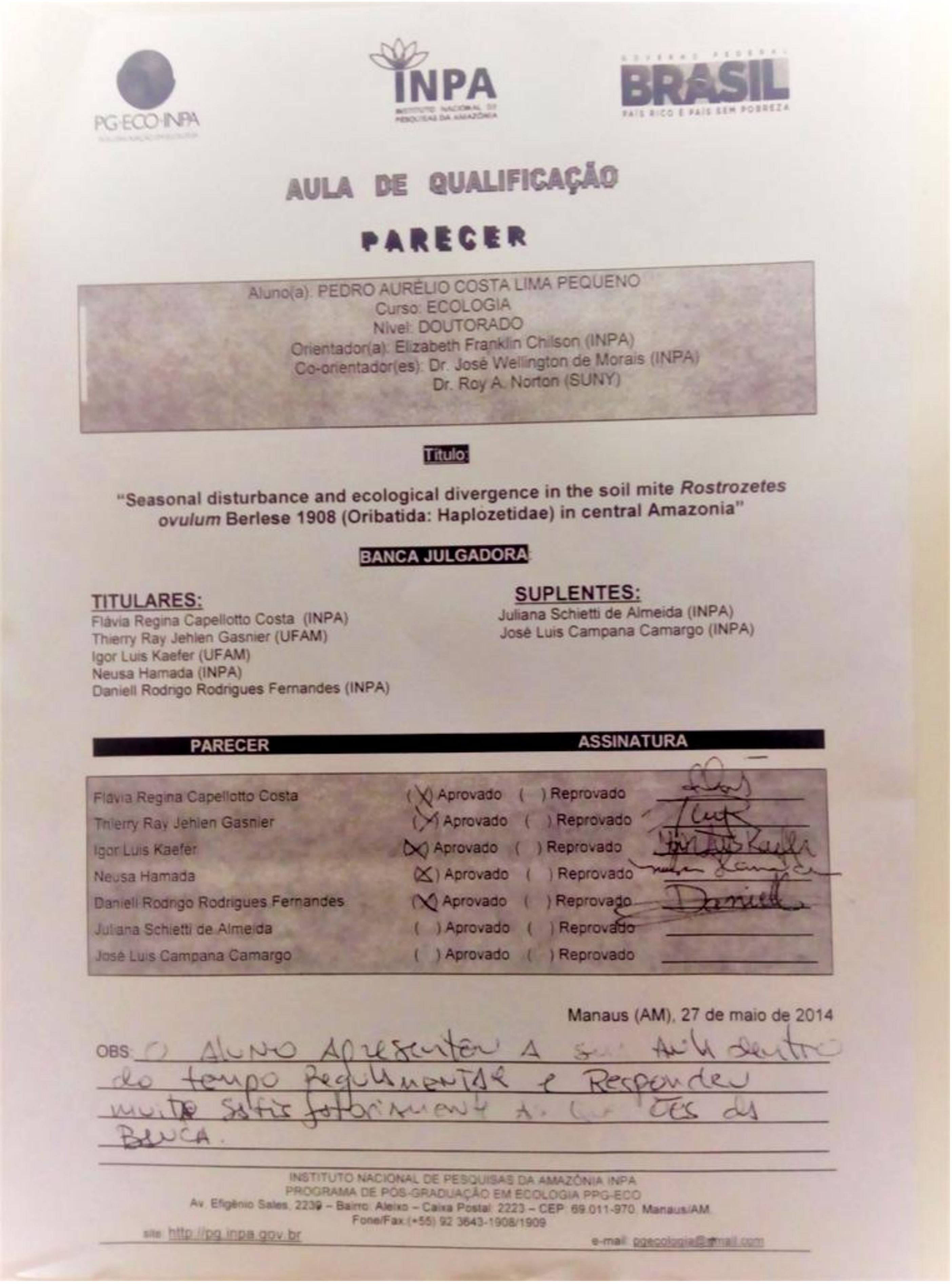

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Nível: DOUTORADO
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Dr. Roy A. Norton (SUNY)

Título:

"Seasonal disturbance and ecological divergence in the soil mite *Rostrozetes ovulum* Berlese 1908 (Oribatida: Haplozetidae) in central Amazonia"

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Manaus (AM), 27 de maio de 2014

OBS: O aluno apresentou a sua aula dentro do tempo regulamentar e respondeu muito satisfatoriamente às questões da banca.

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BRASIL

ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 17 dias do mês de novembro do ano de 2017, às 14:00 horas, no auditório dos PPG's ATU/CFT/ECO, Campus III, INPA/V8. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Flávia Regina Capellotto Costa**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Fabricio Beggiato Baccaro**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Cintia Cornelius Frische**, da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Luiz Ernesto Costa Schmidt**, Universidade do Vale do Rio dos Sinos – UNISINOS, o(a) Prof(a). Dr(a). **Gil Felipe Gonçalves Miranda**, do Instituto Nacional de Pesquisa da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). Igor Luis Kaefer, da Universidade Federal do Amazonas - UFAM, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** de **PEDRO AURÉLIO COSTA LIMA PEQUENO**, intitulado **" EVOLUÇÃO DEBAIXO DO NOSSO NARIZ: DIVERGÊNCIA ECOLÓGICA ENTRE POPULAÇÕES SIMPÁTRICAS DE UM ARTRÓPODE EDÁFICO "**, orientado pelo(a) Prof(a). Dr(a). Elizabeth Franklin Chilson, do Instituto Nacional de Pesquisas da Amazônia – INPA e coorientado pelos(as) Profs(as). Drs(as). José Wellington de Morais, do Instituto Nacional de Pesquisas da Amazônia – INPA e Prof(a). Dr(a). Roy A. Norton, The State University of New York – SUNY.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☐ APROVADO(A)	☐ REPROVADO(A)
☒ POR UNANIMIDADE	☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Flávia Regina Capellotto Costa ____________________

Prof(a).Dr(a). Fabricio Beggiato Baccaro ____________________

Prof(a).Dr(a). Cintia Cornelius Frische ____________________

Prof(a).Dr(a). Luiz Ernesto Costa Schmidt ____________________

Prof(a).Dr(a). Gil Felipe Gonçalves Miranda ____________________

Prof(a).Dr(a). Albertina Pimentel Lima ____________________

Prof(a).Dr(a). Igor Luis Kaefer ____________________

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Coordenação PPG-ECO/INPA