Contents lists available at ScienceDirect

Pedobiologia - Journal of Soil Ecology

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

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ARTICLE INFO

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 spatio-temporal 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 ($3.5 \times 3.5 \times 5$ 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/m² per sampling time. However, over all 180 observations, abundance averaged 58.04 individuals/m² per sampling

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			

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 ($P = 0.07$).

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/m². However, random intercepts varied largely among transects, with estimates of the abundance peak varying from 19.99 to 251.83 individuals/m².

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/m², on average) than in valleys (43.26 individuals/m², 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/m² in plateaus and 3.67 individuals/m² 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
		Month²	−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

(a) (b)
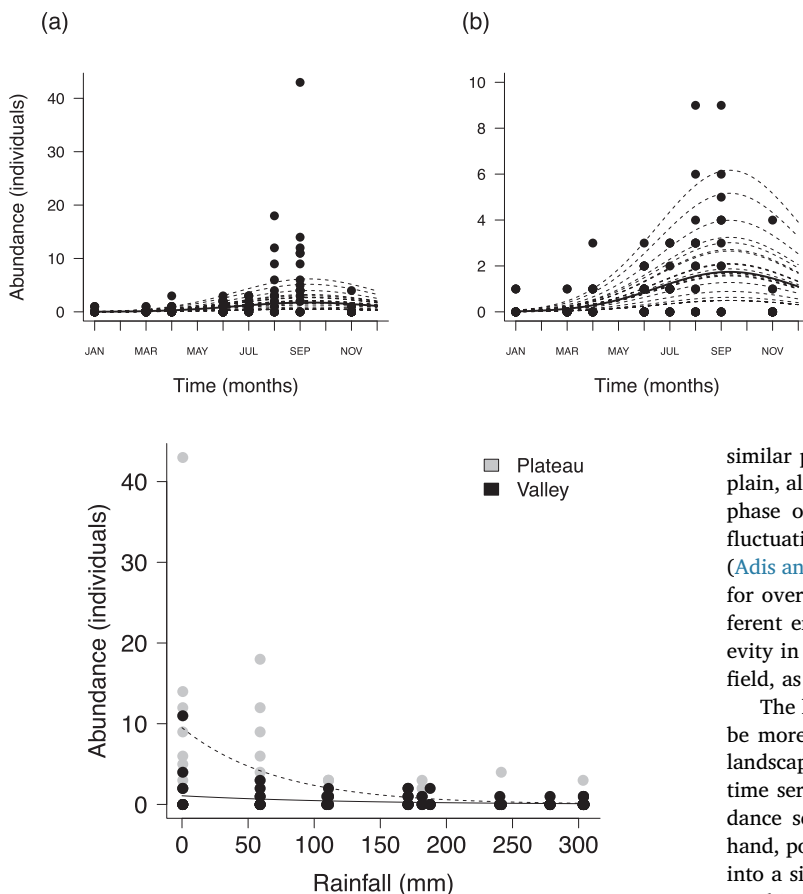
Fig. 1. Seasonality in the abundance of the soil mite *Rostrozetes ovulum* in a central Amazonian rain forest. (a) All data. (b) Same plot, but zoomed in on the concentration of data for better visualization. Each point represents a transect/sampling time combination. Lines represent GLMM fits based 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.

Acknowledgments

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