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

Pedro Aurélio Costa Lima Pequeno[a,*], Elizabeth Franklin[b], Roy A. Norton[c],
José Wellington de Morais[b], Diego R. Guilherme[d]

[a] Ecology Graduate Program, National Institute for Amazonia Research, Manaus, AM, Brazil
[b] Biodiversity Coordination, National Institute for Amazonia Research, Manaus, AM, Brazil
[c] College of Environmental Science and Forestry, State University of New York,1 Forestry Drive, Syracuse, NY 13210, USA
[d] Entomology Graduate Program, National Institute for Amazonia Research, Manaus, AM, Brazil

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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 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).

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