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Essays and Perspectives

Influence of soil granulometry on average body size in soil ant assemblages: implications for bioindication

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ABSTRACT

Soil granulometric composition can impose constraints on ant species living in ground habitats, being an important factor in defining the habitat templet, which describes how certain animal life histories, including the trait of body size, can be selected. The ant fauna plays a central role in soil formation, and a vast literature describes such influence, but not the converse. Along with termites, worms and other invertebrates, these organisms promote the formation of channels, pores, and aggregates that influence gases and water moving through the soil profile. On the other hand, it is important to understand whether soil traits constrain insect colonization, so we here ask how soil traits can influence niche specificities, which seems to be a neglected ecological issue. A literature search using the key words 'ants or Formicidae' and 'soil structure or pedogenesis' revealed numerous references dealing with the influence of ants on soil, but not conversely. We here present a novel geomorphologic approach to habitat templets for two distinct riparian Neotropical ecosystems, based on the amalgamation of soil/sediment analysis with ecological processes and ant species biology. We found that predominance of fine grains favoured the preponderance of small ant species at a threshold of <5 mm in body length. Based on this, we propose the use of a quantitative, theoretically sound, statistical approach to bioindication.

Introduction

Since Hutchinson's classical consideration of evolution as a play performed in the ecological theatre (1965), ecologists have tried to incorporate any type of role within the species and forcing an adaptative explanation, not always valid, to their interactions. However, whether neutral and random (Strong et al., 1984; Hubbell, 2001), or a product of directional evolutionary forces imposed by interspecific competition (Cody and Diamond, 1975's first and second rules of competition and community structuring), species composition and species relative densities are fingerprints of the environment. As such, species and population traits may lead to a practical use, namely bioindicating the existence of certain conditions in ecosystems or their habitats. It follows that species community parameters should reflect ecosystem health and integrity. The baseline for this approach comes from Southwood's (1977) Presidential Address to the British Ecological Society, when he speculated whether habitat would be the "templet for ecological strategies". In other words, he elegantly explained how habitats constrain and define what kind of community must be found in them, based on species specificities.

Further explored by Greenslade (1983), the habitat templet concept was used to better explain life history distributions in nature, and was refined to a simplistic r- to k- to A (for Adversity) strategies triangle. This theoretical framework should be an obvious foundation for the concept of bioindication, since by monitoring what species are found in certain habitats, one could provide a rapid diagnosis of impacts on these habitats. The absence of expected species, or the presence of opportunistic, unexpected species are both facts related to disturbance, and the monitoring of such species for bioindication is likely to be cheaper and quicker to carry out than a full environmental diagnosis.

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Despite this promising idea, the principles of the habitat templet have not been widely adopted as baseline for applied studies of species populations or communities, except in the case of benthic aquatic fauna (Marques and Barbosa, 2001; Marques, 2004). There are two possible reasons for this. On the one hand, the idea of a habitat templet erroneously assumes constancy in the abiotic conditions, and does not consider the counter effect of, for instance, how a species can change the habitat during natural succession. Neither does it consider which species cause the most definitive changes in habitat conditions (Jones et al., 1997). We acknowledge that the difficulty of obtaining data on abiotic and biotic matching conditions renders a direct theoretical approach less palatable for applied ecologists. Still, none of these impediments should hinder attempts to incorporate the habitat templet concept into bioindication procedures.

Members of the soil fauna are among the most diverse components of an ecosystem (Vargas and Hungria, 1997). The soil macrofauna, including ants, spiders, termites, earthworms and others (Bachelier, 1978; Berthelin et al., 1994; Lavelle et al., 1994) are representatives of key functional guilds. Through digging, foraging, building nests, galleries, chambers and corridors, or transporting excavated soil materials, they redistribute organic and inorganic matter across the soil profile. It follows that the macrofauna can be used as a bioindicator of soil quality, since it plays an important role in the regulation of pedogenetic development (Brussard, 1998).

Likewise in a species-engineering (Jones et al., 1997) or a habitat templet (Greenslade, 1983) approach, ants, amongst all taxa, ought to be taken into account when considering soil traits that select species occurrence. However, soil fauna is not always considered in studies of soil beyond a description of community patterns (Andersen and Majer, 2004). Indeed, as far as we know, beyond our work only Yanoviak and Kaspari (2000) considered ant species traits (namely body size) based on habitat templet effects on competition between species. Notwithstanding this, invertebrates are widely used in impact and environmental restoration studies, especially in a bioindicative approach to human impacts (Abbott et al., 1979; Majer, 1983; Pérès et al., 2011; Simmons et al., 2015).

We here review disturbance in soil structure and the usage of ant assemblages as bioindication tools for diagnosing changes in habitats. Then, we illustrate the use of such an approach using two Brazilian examples of ant assemblage response to soil impacts. Finally, we discuss the relevance of adopting a theoretical approach for applied soil ecology studies, based on the assumption that soil granulometry is a key habitat filter, and thus a component of the habitat templet for soil fauna.

Disturbance and soil structure

The soil originates from rock degrading processes or structural rearrangement of a previously transformed matter that composes the earth's surface (Castro, 2008). These changes are caused by chemical, physical and biological factors that influence the rock matrix and cause soil horizon shaping, and thus, heterogeneity due to variations in mineralogical composition, colour, texture, and/or structure (Beljavskis and Juliani, 1986).

The mineral portion of the ground is composed of particles of various dimensions and arrangement in space. These sands, muds and gravels comprise individual particles that, along with organic matter, air and water, constitute what we know as 'soil'. Determining the granulometric distribution of size and proportions of constituent particles is the basis for accurate description of soils. These traits directly affect physical processes taking place in soil, such as transport and deposition, porosity and permeability (Suguio, 1980). It is through knowledge of granulometric distribution that one can infer about the potential for compaction, aeration, transmission of heat, infiltration and water distribution in soil (Prevedello, 1996). Soil traits related to water retention and nutrient availability to plants are major components of edaphic stratification (Silva et al., 2005) and are essential for the diagnosis of soil functioning as well as effects of disturbance.

Various distinct soil features may appear after disturbance. Soils that have recently been exposed or impacted by activities such as mining may have a high infiltration capacity, since their grain structure becomes disarranged. However, if exposed for a long period, soil aggregates are broken up by the kinetic energy of raindrops when they touch the soil surface. These separated particles may form a dense crust a few millimetres thick on the soil surface, further reducing infiltration of water, transmission of heat and gas exchange between soil and atmosphere, and also impacting nutrient cycling (Al-Durrah and Bradford, 1982; Le Bissonais et al., 1989). The compaction process results in decreasing roughness and volume of macropores, thus increasing the density of the sediment (Leite et al., 2004). Soil macro- and micronutrients at the surface become blocked by the thin and compact crust and will not be washed down to the deeper levels. Due to this process, during the rainy season nutrients are leached and over time the process may result in soil nutrient impoverishment, which leads to slow or stagnated natural succession, an issue that may impede habitat restoration.

In disturbed areas, ants contribute to soil recovery, as they promote changes in chemical and physical properties, making soils richer in available nutrients such as nitrogen, phosphorus, potassium, magnesium and calcium (Carlson and Whitford, 1991; Wagner et al., 1997; Lafleur et al., 2005). Furthermore, they mix soil grains by the bioturbation process (Hole, 1961; Lavelle, 1993; Pielström and Roces, 2013). The galleries formed by ants are particularly important in environmental recovery, even after the colony has been abandoned. The network of galleries (or biopores) connecting nest chambers has a significant influence on water infiltration, on soil aeration process and on root penetration, particularly in areas where the upper layer of the soil is compacted (Lobry de Bruyn and Conacher, 1994; Nkem et al., 2000). In ecosystem rehabilitation projects, such as after mining or other severe types of long term disturbance, ants occupy an important role in the regulation of vital processes in soil, creating channels, pores, and aggregates (Coutinho et al., 2003; Lavelle et al., 2006), increasing fertilization (Wu et al., 2013) and causing protection from erosion (Hawksworth, 1991; Doran et al., 1994).

Bioindication by ants

Changes in natural habitats may be detected by monitoring bioindicator species or functional guilds, which consist of those populations (or assemblages of species) that reflect the conservation status of the biotic and abiotic environment. In other words, a taxonomic bioindicator group can reflect changes in impacted habitats, communities or ecosystems, as their ecological requirements change. The more they are representative of overall community diversity and of distinct ecological functions, the better indicators they are (McGeoch, 1998). Ants are considered excellent bioindicators because they are an extremely abundant group, with relatively high numbers of species that are taxonomically treatable, with many specialist species occupying different trophic levels and niches, and many of those species react promptly to changes in the environment (Majer, 1983). Ant diversity is influenced by the diversity and density of plant species (Basset et al., 2012; Queiroz et al., 2013), vegetation physiognomy (especially stratification – Costa-Milanez et al., 2014), as well as by abiotic factors such as

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