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Earthworm functional traits, landscape degradation and ecosystem services in the Brazilian Amazon deforestation arc

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ABSTRACT

Earthworms, as ecosystem engineers, help to mineralize soil organic matter, construct and maintain soil structure, and often stimulate plant growth and protect plants from pests. The aim of this study was (i) to determine the connection between earthworm traits and indicators of soil ecosystem services and (ii) to identify earthworm "response" traits, which are selected by the landscape or changes in the soil, and "effect" traits, which contribute to soil processes. In the southern portion of the state of Parà (eastern Brazilian Amazonia), we sampled earthworms at 135 points distributed among 3 locations, 9 sub-locations and 27 farms (5 sampling points per farm). At each point, three 25 cm × 25 cm soil samples were hand-sorted for earthworms. We measured eight functional traits in 1148 individuals: relative gizzard size, type of typhlosole, length and type of caudal setae, pigmentation, overall length, thickness of septa and musculature in anterior segments. We found a significant, although relatively low, relationship between landscape classes and trait proportions. Earthworm trait proportions significantly covaried with soil parameters and indicators of soil ecosystem services. We did not find significant covariation between earthworm morphospecies and soil ecosystem services. We identified earthworm "response" traits that had been selected and assessed consequences of these changes on effects of earthworm communities (via their "effect" traits) on soil processes and ecosystem services. Typhlosole type, gizzard size and septa thickness were identified as "response" traits selected by soil and landscape conditions. These traits were also identified as "effect" traits for their influence on soil structure. Results indicated a connection between earthworm traits and landscape degradation and soil services, which is a new step toward conceptualizing earthworm ecological studies that go beyond the species level.

1. Introduction

Negative effects of deforestation on earthworm communities in tropical areas of South America are widely documented [1–7]. Although these land-use changes are assumed to influence the soil's supply of ecosystem services [8,9], no clear evidence has been

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observed. Ecological classification has been used to link morphological characteristics with ecological functions to assess the influence of earthworms on ecosystem services [10]. Thus, 'epigeic' earthworms, i.e. small and well-pigmented earthworms that fragment and transform leaf litter in the top soil layer, have been distinguished from 'anecic' earthworms, i.e. larger dorsally-pigmented earthworms that dig vertical burrows and feed in the litter. The former are associated with transforming the litter and the latter are associated with water infiltration, incorporating litter into the soil and soil aggregation. Non-pigmented 'endogeic' earthworms, which feed and live in the soil, contribute most to soil aggregation.

This classification, however, cannot accurately predict effects on ecosystem services and is not easily applicable to families other than Lumbricidae, for which it was created [11,12]. The current recommendation is to consider all functional traits that could determine the response of organisms to environmental conditions and changes and to determine ecological functions, i.e. effects on ecosystem processes, of individuals of each species in a community [13]. Traits are defined as morphological, physiological or phenological characteristics that are measurable at the individual level, from the cell to the whole organism [14]. This approach was recently applied to earthworm communities by using a single set of traits to determine the ecological function of all individuals of the same species [15].

Traits can vary substantially among individuals of a given species, during growth for example, since adults are often 15-40 times larger than newly hatched individuals [16]. Therefore, it is important to assess at least the traits that change with earthworm age and that are carried by individual earthworms. This study estimates effects of community changes following deforestation in Amazonia on earthworm ecological functions via a change in relative proportions of functional traits. We first assessed the extent to which environmental conditions act as filters in selecting a certain set of *response* traits, *sensu* Lavorel and Garnier [13]. We then assessed how this selection of specific *effect* traits influences soil processes by analyzing the covariation between the proportions of earthworm traits in a community and indicators of soil ecosystem services at the same location (e.g. climate regulation via carbon (C) sequestration, water cycle and soil erosion regulation via water infiltration in soil, support for primary production via soil quality and water storage). Functional traits can be assessed for each individual without needing to identify the species, which is complicated when most individuals are juveniles, and adults belong to species (often genera) that have never been described.

As ecosystem engineers, earthworms influence soil organic matter dynamics and soil structure maintenance, which determines all hydrological services. They also stimulate plant growth and can protect plants from pests [9,18,19]. They influence soil structure and processes via their effect traits, *sensu* Lavorel and Garnier [13]. For example, body diameter can determine the diameter of subterranean galleries and the size of stable soil macroaggregates derived from casts deposited in the soil. Environmental changes, which select specific response traits that facilitate adaptation to new conditions, may change the proportions of effect traits and thus alter the intensity and type of processes influenced by the community [20].

The aim of this study was (i) to determine the connection between earthworm traits and indicators of soil ecosystem services and (ii) to identify earthworm "response" traits, which are selected by the landscape or changes in the soil, and "effect" traits, which contribute to soil processes.

The latter are selected by diverse levels of disturbance induced by deforestation and management in the Amazon forest. We assessed consequences of this selection on the effect of earthworms on soil processes and ecosystem services.

We considered earthworm traits that are expected to influence soil processes and measured the values or forms taken by these traits, called attributes [14]. The traits selected influence the ability to burrow and bioturbate (an effect trait) or, like pigmentation (likely a response trait), to survive in the litter and the surface environment. We expect that large earthworms are the most sensitive to deforestation; large anecics and large endogeics (K-strategists) are affected by the disappearance of the litter layer and are sensitive to perturbations that disrupt their habitat. Their relatively long generation time, 1–2 years [16], is probably a greater disadvantage for recolonizing disturbed habitats. We also assumed that the proportion of attributes associated with endogeic earthworms, such as an extended typhlosole, is greater in disturbed landscapes with more pasture than in preserved landscapes.

2. Materials and methods

Earthworm communities were sampled from a wide range of land-use types in the Amazonian deforestation arc (i.e. the area where deforestation is concentrated along the southern edge of the Amazon forest) in the southern portion of the state of Pará, from pristine forests to fallows of different ages, to pastures and cropping systems. We assessed the influence of landscape degradation (as an index) on earthworm traits. Covariations among trait proportions were observed, landscape features were described in a table of landscape metrics, and soil characteristics were analyzed to identify dominant response traits. We tested covariations with indicators of soil ecosystem services determined from soil variables used as a proxy (i.e. climate regulation via C sequestration, water cycle and soil erosion regulation via water infiltration into soil, support for primary production via soil quality and water storage [21]) to identify which of the measured traits could be considered effect traits.

2.1. Study sites

The three study locations (Palmares II, Maçaranduba and Pacajá, Fig. 1, Table 1) had different historical and landscape conditions: deforestation began in 1990, 1994 and 1997 at the three locations, respectively. The different historical and socio-economic conditions have greatly influenced the composition of the landscape and the three locations. Pacaja, Maçaranduba, and Palmares II represent three successive steps in the landscape degradation process. We selected three groups of three adjacent farms in each area. On each of the 27 farms, five sampling points were located 200 m apart along a transect extending diagonally across the farm, thus representing a total of 135 points [22–25].

2.2. Earthworm sampling

A modified version of the Tropical Soil Biology and Fertility (TSBF) protocol [26] was used from April to June 2008 to sample earthworms and other soil macrofauna. At each of the 135 points, a central soil monolith (25 cm × 25 cm, 20 cm deep) was taken, as were two additional soil monoliths (25 cm × 25 cm, 10 cm deep) located 5 m east and west, respectively, of the central monolith. Thus, one sample unit was composed of three monoliths, yielding a total of 405 monoliths. Earthworms found in each monolith were hand-sorted and preserved in a 4% formaldehyde solution. Due to problems preserving earthworms, only 116 points could be used in this study.