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DNA barcoding reveals diversity patterns of earthworm communities in remote tropical forests of French Guiana

Thibaud Decaëns [a, *], David Porco [a], Samuel W. James [b], George G. Brown [c], Vincent Chassany [d], Florence Dubs [e], Lise Dupont [f], Emmanuel Lapied [g, h], Rodolphe Rougerie [i], Jean-Pierre Rossi [j], Virginie Roy [k]

[a] EA 1293 ECODIV, University of Rouen, SFR SCALE, UFR Sciences et Techniques, bâtiment IRESE A, F-76130 Mont Saint Aignan, France
[b] Department of Biology, University of Iowa, Iowa City, IA 52242, USA
[c] EMBRAPA Florestas, Empresa Brasileira de Pesquisa Agropecuária (Embrapa), Colombo, PR, Brazil
[d] University of Paris Diderot, 4 rue Lagroua Weill-Hallé, F-75205 Paris Cedex 13, France
[e] UMR IEES Paris, IRD, 32 Avenue H. Varagnat, F-93143 Bondy Cedex, France
[f] UMR IEES Paris-Biodis, Université Paris-Est Créteil, 61 avenue du Général de Gaulle, F-94010 Créteil Cedex, France
[g] Bioforsk Soil and Environment, Norwegian Institute for Agricultural and Environmental Research, Fr. A. Dahlsvei 20, 1430 Ås, Norway
[h] Norwegian University of Life Sciences (NMBU), Isotope Laboratory, Fougnerbakken 3, 1430 Ås, Norway
[i] Muséum national d'Histoire naturelle, UMR 75205 — ISYEB Institut de Systématique, Evolution, Biodiversité, 45 rue de Buffon, CP50, 75005 Paris, France
[j] UMR 1062 CBGP, Centre de Biologie pour la Gestion des Populations, INRA, F-34980 Montferrier-sur-Lez, France
[k] UMR IEES Paris-DIIM, Université Paris-Est Créteil, 61 avenue du Général de Gaulle, F-94010 Créteil Cedex, France

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ABSTRACT

Despite representing a key component of terrestrial biota, soil invertebrates in tropical rainforests have been poorly studied from both a taxonomic and an ecological perspective when compared to other groups of terrestrial animals. We sampled earthworm communities in a range of sampling locations in two different study sites of the Nouragues Natural Reserve in French Guiana, focusing on lowland to plateau and hilltop forests as well as on savannah-like vegetation of the Nouragues granitic inselberg. We used the barcode region of the COI gene to delimit Molecular Taxonomic Units (MOTUs), further validated using species-level diagnostic morphological characters. A total of 651 sequences was obtained, most of them corresponding to juveniles that cannot be identified to the species level from morphology alone. We found a total of 48 MOTUs, and both rarefaction curves and diversity estimators (Chao1 and ACE) suggested that 60 species could occur in the study area, representing the highest earthworm richness ever recorded worldwide. Beta-diversity analyses highlighted a strong species turnover between sampling locations. Except in a few specific cases, species richness was usually limited to 12 species at the scale of a given location, which likely indicates the influence of competitive interactions during community assembly process. Community structure was dominated by species living in the upper soil layers and in surface microhabitats, with some of them able to colonize epiphytic soils up to more than 40 m above ground level. These results suggest the importance of long-term diversification processes and current ecological factors for the structuring and the diversity of earthworm communities in tropical rainforests of French Guiana.

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1. Introduction

Tropical rainforests, whilst only covering 6–7% of the worldwide continental surfaces, have been popularized as the most emblematic ecosystems from a biodiversity viewpoint (Wilson, 1988). Understanding the patterns and drivers that govern tropical biodiversity inspired generations of ecologists, allowing the emergence of new concepts leading to fundamental advances in theoretical and evolutionary ecology (Chazdon and Whitmore, 2002).

* Corresponding author. Present address: Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175 CNRS, University of Montpellier, 1919 Route de Mende, 34293 Montpellier Cedex 5, France.
E-mail address: thibaud.decaens@cefe.cnrs.fr (T. Decaëns).

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However, tropical biodiversity studies historically focused on conspicuous vertebrates and higher plants, neglecting most invertebrate taxa that represent the vast majority of the world's eukaryotic diversity (May, 2011). Studying invertebrate community patterns in tropical rainforests is currently challenged by the huge number of locally co-occurring species, and by the weakness of our taxonomic knowledge in many groups (Godfray et al., 1999; Adams et al., 2014). In this context, considering soil communities represents a major challenge, as they harbor a vast diversity of species (Decaëns, 2010) which activities are essential for a large range of key ecological processes (Lavelle et al., 2006). Paradoxically, soil invertebrates have been given poor taxonomic and ecological coverage by comparison with aboveground organisms (Decaëns, 2010), resulting in a global taxonomic impediment for soil biodiversity studies (André et al., 2001). As a consequence, we know little about tropical soil invertebrate community structure and species richness along key environmental gradients.

DNA barcoding, using a fragment of the mitochondrial gene cytochrome c oxidase I (COI) as a standard genetic marker for species detection and identification in animal kingdom (Hebert et al., 2003), represents a potential solution to remove this taxonomic impediment. Given the limitations and the potential pitfalls of defining species boundaries through a single-gene approach (Rubinoff and Holland, 2005; Wiemers and Fiedler, 2007), several authors advocated for the use of an integrative taxonomic approach combining different sources of evidence (e.g. morphological characters, ecological features or geographic distributions) in addition to molecular data (Dayrat, 2005; Puillandre et al., 2012). Nevertheless, since the seminal paper of Hebert et al. (2003), a growing number of studies have demonstrated the potential of DNA barcodes, alone or combined with other taxonomic data, as a tool to alleviate the taxonomic impediment and increase the pace of biodiversity pattern description (Puillandre et al., 2012; Smith et al., 2013; Lees et al., 2014). DNA barcoding can also be useful in describing community patterns in poorly studied regions, and/or for groups of organisms with poorly resolved taxonomy or with strong identification difficulties (Tanzler et al., 2012; Young et al., 2012; Porco et al., 2013). Obtained systematically for a large number of individuals collected across an ecologically meaningful sampling design, it can be used to delimit Molecular Operational Taxonomic Units (MOTUs) usable as reliable species proxy to estimate taxonomic richness and to describe community patterns at different spatial scales (Blaxter et al., 2005). In soil communities, this approach has now been used in several studies focusing on e.g. collembolans (Porco et al., 2013), ants (Smith et al., 2005) and mites (Young et al., 2012).

In this study, we used DNA barcodes to describe earthworm assemblages in a remote forest area of French Guiana. Despite being the focus of a prolific literature documenting their contribution to key ecosystem processes, earthworms are characterized by a strong taxonomic deficit which represents a severe bottleneck to develop basic studies of their community ecology (Decaëns et al., 2013). In the tropics, only a few studies have described the structure of earthworm assemblages in natural ecosystems (Lavelle, 1978; Nemeth, 1981; Fragoso, 1985; Jiménez, 1999; Feijoo, 2001). We conducted two successive earthworm surveys in a range of habitat types in the Nouragues Nature Reserve to describe species richness levels and community patterns at different scales. Samples were analyzed using a combination of DNA barcoding, morphological and ecological data. The operational species concept is based on the assumption of separately-evolving populations leading to the emergence of divergent lineage (de Queiroz, 2007). Our surrogate of that is an integrative combination of molecular species (MOTUs) delimited using COI sequences and morphology based on species-level diagnostic characters. These surrogate taxa were used to describe the structure of earthworm communities and to explore their assembly rules.

2. Material and methods

2.1. Study sites

Sampling was conducted in June 2011 in the Pararé and in January and June 2011 in the Inselberg research stations (RS) of the Nouragues Nature Reserve, in French Guiana. Climate is tropical humid with mean annual rainfall of 3000–3250 mm, mainly distributed during the wet season between December and June, and average maximum and minimum monthly temperatures are 20.3 °C (19.7–21 °C) and 33.5 °C (32.1–35.8 °C), respectively.

Inselberg RS is located at the piedmont of the Nouragues granitic inselberg mountain culminating at 411 m above sea level (base camp WGS84 coordinates: N4°05′17.73″/W52°40′47.90″). Vegetation around the base camp consists of a patchwork of different types of tropical rainforest and 'rocky savannah' vegetation on the slopes of the inselberg. Pararé RS is 6400 m from the Inselberg RS, and is located on the edge of the Arataye River (base camp WGS84 coordinates: N4°2′17.30″/W52°40′22.31). Vegetation around the base camp is dominated by tropical rainforest on flooded to well-drained soils depending on topography. In the vicinity of each of the two base camps (SI Fig. 1), we sampled earthworms in a total of 11 distinct sampling locations representing the main types of vegetation available. The main characteristics of these locations are given in Table 1 and SI Table 1.

2.2. Earthworm sampling

For each sampling location, we sampled earthworms at one to six sampling points, depending on the relative representation of the corresponding habitat in the landscape. Overall, our sampling design allowed for a consistent survey of the range of ecosystems found in the vicinity of each of the two research stations. Each sampling point consisted of a 50 m-radius circle centered on a geo-located point and in which earthworms were sought in all available and attainable microhabitats during a fixed period of six researcher-hours. All life stages (i.e. adults, juveniles and cocoons) were collected, in four main types of microhabitats considered as suitable for earthworms (Fragoso and Rojas-Fernandez, 1996): (1) organo-mineral and holorganic soil layers, and (2) sandy to muddy sediments of stream banks were dug out with a spade and hand-sorted; (3) litter accumulations and decaying trunks on the soil surface were prospected by carefully sorting them with a small spade or a machete; (4) 'epiphytic soils' (i.e. organic matter accumulation in epiphytic plants and hollow trees) up to 40 m above the surface were brought to ground level to be hand-sorted. Specimens collected at a given point were kept alive in separate boxes corresponding to the in which they were found (i.e. soil, river bank sediments, decaying trunks or epiphytic soils).

2.3. DNA barcoding

Specimens were cleaned with water before being killed and fixed in 100% ethanol. For large specimens, the solution was changed once after 24 h in order to insure an efficient fixation. Once fixed for at least 24 h, the specimens collected at a given point and microhabitat were broadly sorted into 'morpho-groups' based on external morphological characters, mainly size, pigmentation, and clitellum and genital markings positions and shapes in adults. We then selected up to 5 specimens per morpho-group for DNA barcoding. Although these groups were imperfectly defined taxonomically (e.g. adults and juveniles were usually placed in different

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