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Trophic interactions among soil arthropods in contrasting land-use systems in Kenya, studied with stable isotopes☆

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ABSTRACT

Understanding how land use intensification changes organism communities and trophic interactions in soil is important for development of sustainable agriculture and forestry.

We analysed the food web of soil arthropods with help of natural $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios ($\delta^{13}C$ and $\delta^{15}N$) in two habitats in the Kenyan Highland – a natural forest and an agricultural site on former forest land. Aims of the study: (1) to describe the structure and feeding relationships in the two systems for major soil arthropod groups, (2) to find differences in feeding strategies within major arthropod groups, (3) to determine if soil arthropod groups have the same trophic positions in forest and agricultural soil, (4) to evaluate if $\delta^{13}C$ and $\delta^{15}N$ can be explained by additional reasons, e.g. the physiology and C:N ratios of organisms.

This is one of few studies of the trophic structure of soil arthropod communities in tropical ecosystems. It confirms that the structure is similar to comparable systems in the temperate zones. There was a large variation in $\delta^{15}N$ among families of Oribatida, Mesostigmata and Collembola (the most common groups) indicating great variety in feeding ecology. Collembola and Diplopoda had comparatively high $\delta^{15}N$, indicating a contribution of animals to the diet. Although lower abundance and diversity of arthropods in the agricultural soil, the trophic positions of particular taxa, indicated as $\delta^{15}N$ level, were similar to the forest. The $\delta^{13}C$ values were negatively correlated to the C:N ratio, therefore increasing values of $\delta^{13}C$ with trophic level could not be demonstrated.

1. Introduction

Deforestation and conversion of forest areas to agricultural land leads to decreased abundance and diversity of many groups of organisms in the soil. This impoverishment is due to disturbances to the soil as well as to decreased and less varied input of plant material, which forms the base for the grazer and decomposer food webs [6,22]. In the organism communities of soil ecosystems, there is a high degree of generalism and omnivory in resource-use among decomposer organisms and thus there is reduced competition among species in combination with a highly heterogeneous environment in the soil [59]. Therefore, some researchers claim that reduced species diversity will have little effect on ecosystem functions such as decomposition [4,18]. But many recent studies find that reduced abundance and diversity of soil organisms leads to reduction of many ecosystem services [7]. Because of this, understanding how land use intensification changes the composition of soil organism communities and subsequently affects the trophic interactions in soil is important for development of sustainable practice of agriculture and forestry. Not the least in tropical systems that now are rapidly transferred into agricultural land.

Feeding relationships among soil-living arthropods and other soil animals are hard to study because of the small size and the fact that they live in an opaque medium. Direct observations in the animals' natural habitats are difficult or almost impossible, but lab-based observations and food selection experiments have provided valuable information [54]. However, such results cannot be directly transferred to the natural habitat of the animals where a more diverse offering of food items that varies in time and space can be expected.

Analyses of gut contents can be done by dissection or by

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observations under the microscope [2,3,64]. Modern molecular methods, e.g. PCR analysis, have taken gut content analysis even further, and an increasing body of literature has used such techniques to enhance our knowledge of several groups of soil animals. Although techniques have improved [16], the small body size of animals such as Acari and Collembola and the associated small gut content cause methodological problems. Another limitation on the use of such technology is the need to sequence and find primer sites for all of the target species that might comprise the diet of a predator or scavenger. In addition, these kinds of methods do not tell what part of the ingested food items are assimilated and what parts will only pass through the gut and be discharged as faeces [33].

Stable isotope analysis has now become a commonly used tool for ecological studies of feeding relations [5,62]. On average, the heavier isotopes ^{13}C and ^{15}N are enriched relative to the lighter isotopes of the same elements at each step of the food chain in the tissue of an organism relative to its food source, and each trophic level is traditionally associated with a 1.0‰ point of enrichment for ^{13}C and 3.4‰ point of enrichment for ^{15}N [42]. Recent studies have modified these values, however, and according to a meta-analysis by Vanderklift and Ponsard [63] the enrichment of ^{15}N is 2.54‰ points per trophic level. This technique also has its pros and cons. For example, enrichment between trophic levels can vary depending on the organisms involved and such factors as the age and condition of a particular individual of a species and its lipid content, since lipids are depleted in ^{13}C. Variation of ^{13}C and ^{15}N ratios of organisms not only with their trophic level but also with their C:N ratios (which among other factors depends on the lipid content) has been found in many studies, e.g. Refs. [23,51,52]. Concerning ^{15}N, enrichment also depends on the N-excretion system of different organism groups and in what chemical form N is excreted [63]. Since the tissue composition and excretion systems vary between systematic groups the uncertainty in interpretations of results will increase with number of groups involved. A mixed diets of organisms and organic matter from a variety of environments will add uncertainty to the natural abundance of isotope ratios and it will therefore not be possible to assign a certain trophic position of an organism to a specific diet. However, the analysis of a community of certain types of organism groups will give a broad picture of the feeding relationships in a food web. This can be used for comparisons of the conditions in different environments and for tracing changes induced by environmental impacts [9]. Most studies of food web structures of soil arthropod communities studied with C and N isotope ratios have been done in temperate ecosystems. For example, Scheu and Falca [55] analysed the whole food web of soil micro- and macroarthropods of two beech forest with different soil type, while Crotty et al. [11] included micro- and macroarthropods as well as Nematoda, Oligochaeta and Gastropoda in a study of soil food webs in grassland and woodland. These mentioned studies embrace several systematic groups but most studies are limited to one or a few groups, e.g., [35,40,56]. Only a few studies concern tropical soil ecosystems and then concentrated on macrofauna such as Hymenoptera and Isoptera but omitting microarthropods such as Collembola and Acari [8,28,29].

In the present study, we analysed the natural $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios ($\delta^{13}C$ and $\delta^{15}N$) in the community of soil arthropods and its food base of litter, roots and soil organic matter from two different habitats in the Kenyan Highland, a natural forest and an adjacent agricultural site on a former forest land. The aims of this study were (1) to increase our knowledge of the structure and feeding relationships of soil arthropods in the belowground food webs of a tropical highland forest and how these changed when the forest land was converted to agricultural land, (2) to determine if differences in feeding strategies can be found within major taxonomic groups of arthropods, and to compare this information with knowledge obtained in earlier studies performed with stable isotopes or with other techniques, (3) to determine if soil arthropod groups have the same or different positions in the food web of the more complex and species-rich ecosystem of forest soil compared to the simpler and disturbed system of agricultural soil, and (4) to evaluate to what extent $\delta^{13}C$ and $\delta^{15}N$ found in soil animals and substrates can be explained by trophic positions or other reasons such as the physiology and C:N ratios of animal groups.

2. Materials and methods

2.1. Site description

The study was carried out in two sites in Embu County, Kenya, a forest site and an agricultural site. In the forest site, soil samples for arthropod extraction were taken at 2065 m above sea level in Irangi Forest on the slope of Mount Kenya. The site lies along longitude 37°28′E and latitude 0°20′S. This is a protected natural forest that extends up to the timber line at the border of Mt. Kenya National Park, and it is dominated by the tree species *Cordia africana* (Boraginaceae), *Ocotea usambarensis* (Laruraceae), *Podocarpus falcalus* (Podocarpaceae), *Trichilia emelica* (Meliaceae) and *Vitex keniensis* (Verbanaceae).

In the agricultural site, soil samples for arthropod extraction were taken from a small-holder agricultural field grown with Napier grass (*Pennisetum purpureum* Schumach) in Kibugu Village of Embu County at 1930 m above sea level. The site lies along longitude 37°21′E and latitude 0°27′S. The farmlands are highly fragmented, and intensive cultivation is practiced with high application of inorganic fertilizers. The main crops grown include maize, beans, Irish potatoes, kales, cabbages, bananas, and animal fodder such as Napier grass.

The distance between the two sampling sites was ca. 8 km. They were chosen because they were appointed bench mark sites of the Below Ground Biodiversity (BGBD) Project [45]. The entire study area is a tropical highland and midland forest criss-crossed by hills and valleys [34]. It receives a bimodal rainfall pattern with rains typically occurring from March to June (Long rains) and from October to December (Short rains). Total annual rainfall is between 1200 mm and 1500 mm, and average temperature ranges between 14° C and 19.5° C. The soils are mainly Humic Nitisols derived from volcanic rocks [20,31] and are deep and well drained with clay texture (% sand, clay, silt: 1, 22 and 75). The soil in the forested site is rich in humus and acid with total C-content of 5.6% and pH 3.9. The agricultural site has C-content of 3.5% and pH 4.2 [45].

2.2. Sampling and analysis

Large numbers of soil arthropods were collected at both sites by sampling of the upper 10 cm of the litter and soil profile on several occasions during September and October 2008. The soil was collected using a steel corer with an internal diameter of 5 cm and at a depth of 5 cm including the organic horizon, and the samples were transported to the lab where soil arthropods were extracted from composite samples big enough to fit into Tullgren funnels with a diameter of 15 cm [43]. The arthropods were collected in 100 ml plastic beakers containing 50 ml of 70% salt solution. Ethanol was not used because it can alter ^{13}C values [61]. Collembola, Oribatida mites, and Mesostigmata mites, which were the predominant groups of arthropods, were sorted into families while other groups such as insects and myriapods were sorted into higher taxonomic levels. The collembolan identification was based on Fjellberg [19] and Hopkin [26,27], and mite identification was based on Krantz and Walter [37]. The specimens were subsequently