

The Hidden Oases: Unveiling Trophic Dynamics in Namib's Fog Plant Ecosystem

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Abstract

The Namib Desert is a hyperarid coastal desert where fog is a major moisture source. We hypothesized that the fog-harvesting grass *Stipagrostis sabulicola* establishes an important ecological niche in the extreme Namib Sand Sea ecosystem, referred to as "Fog-Plant-Oases (FPO)". Using a combination of extraction methods, we collected and described the above- and belowground FPO invertebrate communities and inferred their trophic feedings based on stable carbon and nitrogen isotope values. Our findings revealed a complex trophic structure and a unique food web, all of which revolve around a single fog plant as the primary producer. We demonstrated that *S. sabulicola* serves as the primary energy source for the aboveground food web, encompassing a diverse range of trophic levels. Nevertheless, the distinctive stable isotope values of bacterial- and fungal-feeding nematodes indicated the separation of the aboveground niche, which is primarily sustained by *S. sabulicola*, from the belowground niche, where wind-blown sediments serve as the main energy source. These findings further accentuate the role of *S. sabulicola* not only as a primary producer but also as a source of moisture and habitat provider for belowground invertebrates.

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Introduction

Fog oases are fertile vegetation islands that rely on fog condensation for their water supply. They have been widely studied in the *lomas* formation in Peru and Chile (Peru & Péfaur, 1982; Pinto et al., 2006; Rundel & Dillon, 1998), in the relic forests Fray Jorge (30°S) at the top of the coastal range (400 – 650 m ASL) in Chile (Gonzales et al., 2023), the redwood forest *Sequoia sempervirens* in northern California (Dawson, 1998) and the cloud forests of the central South Arabian mountains of Yemen and Oman (Ball & Tzanopoulos, 2020). In the present study, we investigated "Fog-Plant-Oases" (FPOs), which operate on a significantly smaller scale and revolve around individual plants compared to previously studied fog oases that function at the community or ecosystem level. Beneath single grass tussocks of a fog-harvesting plant, soil hammocks or biogenic hillocks were formed, creating isolated islands with moisture and food availability (Danin, 1991). The formation of soil hammocks is postulated to create stable conditions that encourage the utilization and colonization of such FPOs by other species as well as support the growth of the plant itself. Nonetheless, the function of FPOs, particularly by the fog-harvesting specialist *Stipagrostis sabulicola* (*Poaceae*) (Ebner et al., 2011), as trophic hotspots for above- and belowground invertebrates have not been examined.

The Namib Desert is a hyperarid coastal desert in which fog precipitation serves as a significant moisture source (Frossard et al., 2015; Henschel & Seely, 2008; Lancaster & Seely, 1984). At our study area in the Namib Sand Sea, near Gobabeb (23°34'S 15°02'E), fog from the Atlantic Ocean is a more regular moisture source (39 mm mean annual condensation) than rainfall (21.2 mm mean annual precipitation) (Henschel, 2000). Advection fog condensation, where the moisture is derived from evaporation over the South Atlantic Ocean and transported inland by onshore winds, is mainly influenced by the distance from the coast and elevation (Mitchell et al., 2020). To cope with the extreme dryness, a considerable number of endemic species of the flora and fauna of Namib have adapted to exploit atmospheric moisture (Mitchell et al., 2020). An excellent example of how organisms adapted to extreme aridity in the Namib Desert and even shaped their environment is the formation of FPOs by the perennial endemic grass *S. sabulicola*. As shown previously, *S. sabulicola* possesses specialized leaf structures that are highly effective at condensing moisture from the air (Ebner et al., 2011; Roth-Nebelsick et al., 2012). Belowground, *S. sabulicola* has a shallow but extensive root system for effective anchoring in the unstable and highly dynamic windblown sand and uptake of moisture condensing on the sand surface (Louw & Seely, 1980). Overall, these studies have shown the distinctive morphological characteristics that enable *S. sabulicola* to utilize fog water efficiently and stabilize Aeolian sand.

The trophic structure in an ecosystem depicts its energy and nutrient transfers, commonly studied and illustrated through its food web (Holt & Loreau, 2002). Despite their major importance in global biogeochemical cycling, the above- and belowground food webs of ecosystems are still poorly understood, mainly due to the huge diversity of soil-dwelling and aboveground organisms of which many are general feeders (Crotty et al., 2014; Potapov et al., 2019; Scheu, 2002). This is exacerbated by the fact that food web studies are focused on certain land uses and climate regions, such as agricultural lands and temperate ecosystems (Crotty et al., 2014; Potapov et al., 2019; Scheu, 2002). Therefore, there remains a need to continue exploring the trophic structure of both soil-dwelling and aboveground animal communities, particularly in arid and hyperarid ecosystems as they cover a high proportion of the Earth's surface and due to their sensitivity to climate change (Nielsen & Ball, 2015; Quoreshi et al., 2022; Whitford W. G., 1996). Previously, only a couple of studies employed stable isotope analysis in understanding the belowground food web in a hyperarid desert, including the investigation of the diet of soil nematodes and tardigrades under biological soil crusts in the arid Southwest of US (Darby & Neher,

2012) and the study of the diet of nematodes, tardigrades, rotifers, and microarthropods in the McMurdo Dry Valleys in Antarctica (Shaw et al., 2018).

Our study presents the community composition and abundance of previously unexplored above- and belowground invertebrates found around the *S. sabulicola* FPOs. We hypothesized that the fog-harvesting efficiency of *S. sabulicola* facilitates important ecological niches within the Namib Sand Dune ecosystem. Additionally, we proposed that the plant litter from *S. sabulicola* serves as the primary carbon source for the FPO trophic structure, which fuels carbon flow from lower to higher trophic levels. To test these hypotheses, we aimed to measure the natural variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of above- and belowground invertebrates of the *S. sabulicola* FPOs, and to evaluate its trophic connections and food web. Isotopic analysis is based on the premise that the stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of above- and belowground invertebrates reflect their diet compositions. This can be used to determine their trophic positions i.e., detritivores, secondary decomposers, herbivores, or predators within the soil web (Ponsard & Ardit, 2000; Vanderklift & Ponsard, 2003). Combined with isotope mixing models, a finer resolution of their diet compositions can be achieved (Govan et al., 2023; Parnell et al., 2013; Post, 2002). In addition, due to the lack of rainfall that activates microbial decompositions in this hyperarid ecosystem (K. Jacobson et al., 2015; K. M. Jacobson & Jacobson, 1998), we further aimed to identify the main primary decomposers of the *S. sabulicola* FPOs by estimating the contributions of plant litter in their diets.

Results

Diversity and abundance of FPO fauna

Aboveground fauna

The overall composition of non-flying or poor flying arthropods were evaluated by bush-beating. Rapid flyers such as Diptera and Hymenoptera often escaped and thus were mostly not studied. Collected arthropods included: oribatid mites (*Zygoribatula* sp., 100 specimens), beetles (*Cybocephalus* sp., 17 specimens, *Exochmus flaviventris*, 1 specimen), thrips (*Haplothrips* sp., 15 specimens), barklice (*Liposcelis* sp., 14 specimens), weevils (*Sibinia* sp., 13 specimens), pseudoscorpions (*Nanolpium* sp., 9 specimens), leafhoppers (*Deltocephalinae* sp., 5 specimens), jumping spiders (*Salticinae* sp., 2 specimens), ground sac spiders (*Thysanina* sp., 1 specimen), and parasitoid wasps (*Haltichellinae* sp., 2 specimens). Peeling of plant stems revealed the occurrence of armoured scale insects (Diaspididae) and mealybugs (*Pseudococcidae* sp.) and again the oribatid mite *Zygoribatula* sp., under the leaf sheath near the nodes. Details on the taxonomic assignment of these species are provided in Appendix 1. Further groups observed on the leaves of *S. sabulicola*, but not studied in detail, included red velvet mites (Trombididae), predatory mites (Gamasina), and more insects: cockroaches (Blattodea, 1 specimen), grasshoppers (Orthoptera, 1 specimen), true bugs (Heteroptera, 1 specimen), flies (Diptera, several spp.) and parasitoid wasps (Hymenoptera, several spp.).

Supplementary collection of dune surface dwellers that frequently visit *S. sabulicola* included dune ants (*Camponotus detritus*), which tends scale insects and leafhoppers to collect honeydew (Curtis, 1985b). These ants are more abundant on the base dunes as well as on the dune slope as compared to the high dunes. Ten individuals of tenebrionid beetles consisting of *Onymacris plana* (4 specimens), *Physadesmia globosa* (3 specimens), and *Onymacris laeviceps* (3 specimens) were collected both from the high dunes as well as from the dune base near the Kuiseb Riverbed. As a comparison to the *S. sabulicola* food web, two individuals of blister beetles *Hycleus zigzagus* were included, which were the herbivores of the !Nara melon (*Acanthosicyos horridus*) that also occurs on the base of the dunes. *A. horridus* is a perennial endemic shrub and another potential fog-harvesting FPO that grows alongside *S. sabulicola* at the base of Namib dunes.

Belowground fauna

A total of 5233 nematode individuals with a total biomass of 913.4 μg biomass (fresh weight) were extracted through wet extractions (Baermann method). Most individuals were found in soils (dune sands) under mature FPOs with the highest density in deeper soil layers (30-50 cm depth). The nematodes were predominantly bacterial feeders (84.8% of overall biomass) represented by the genera *Acrobeles*, *Cephalobus*, *Cervidellus*, *Chiloplacus*, *Elaphonema*, *Panagrobelus*, *Panagrolaimus*, *Zeldia*, and some juvenile *Mesorhabditidae* and *Diplogastridae*. Fungal-feeding nematodes contributed to 14.7% of overall nematode biomass and consisted of *Aphelenchoides*, *Aphelenchus*, *Ditylenchus*, *Paraphelenchus*, and a few *Tylenchidae*. As a third feeding group, omnivorous nematodes were detected only sporadically, but due to their large body size still accounted for 0.5% of overall nematode biomass. Tardigrades were extracted from only 3 of the 84 soil samples. They belonged to the genus *Hexapodibius* and were found with 3, 5, and 5 specimens under matured FPOs at 5-10 cm soil depth. Also, some mites (Pediculochelidae sp.) were found in very low numbers. Dry

extractions (Berlese method) of another subset of 84 soil samples did not yield any animals, and only small amounts of nematodes, which were not analysed, were caught in underground pitfalls. Flotation (84 samples) yielded altogether 121 mites (Micropasmmidae sp., Pediculochelidae sp., and some Astigmata (not further analysed)) and the remains of a single springtail (cuticle of an *Entomobryidae*).

Stable isotope values

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of basal resources

The average $\delta^{13}\text{C}$ values of different parts of *S. sabulicola* spanned only 1.4‰ between -13.7 and -15.1‰ (Table 1). The fresh leaves were ^{13}C -depleted ($\delta^{13}\text{C} = -15.1 \pm 0.7\text{‰}$) compared to dead leaves ($\delta^{13}\text{C} = -14.0 \pm 0.6\text{‰}$) and dead leaves with visible fungal colonization ($\delta^{13}\text{C} = -14.0 \pm 0.5\text{‰}$). Belowground, plant roots had isotopic values of $\delta^{13}\text{C} = -14.1 \pm 0.3\text{‰}$, and rhizosheaths $\delta^{13}\text{C} = -13.7 \pm 0.4\text{‰}$. Soil detritus (light fraction organic matter) extracted from hummocks of mature FPOs had $\delta^{13}\text{C} = -14.3 \pm 0.2\text{‰}$ values. The average $\delta^{15}\text{N}$ values of different parts of *S. sabulicola* spanned almost 4‰ between -1.9‰ and 2.0‰. The $\delta^{15}\text{N}$ of fresh leaves were close to the atmospheric $\delta^{15}\text{N}$ value of $\delta^{15}\text{N} = 0.2 \pm 1.5\text{‰}$. Dead leaves ($\delta^{15}\text{N} = -1.9 \pm 1.6\text{‰}$) and dead leaves with visible fungal colonies ($\delta^{15}\text{N} = -0.7 \pm 2.5\text{‰}$) were ^{15}N -depleted when compared to fresh leaves. Belowground, plant root ($\delta^{15}\text{N} = 0.1 \pm 1.4\text{‰}$) and rhizosheath ($\delta^{15}\text{N} = 0.8 \pm 0.4\text{‰}$) were ^{15}N -enriched in comparison to fresh leaves; while dead leaves with soil detritus ($\delta^{15}\text{N} = 2.0 \pm 1.2\text{‰}$) were enriched in $\delta^{15}\text{N}$ values compared to plant samples.

Compared to *S. sabulicola*, which had $\delta^{13}\text{C}$ values typical of C_4 plants, the $\delta^{13}\text{C}$ values of *A. horridus* litter resembled those of typical C_3 plants ($\delta^{13}\text{C} = -21.7 \pm 0.8\text{‰}$). Soil detritus under *A. horridus* ($\delta^{13}\text{C} = -17.1 \pm 1.2\text{‰}$) were markedly ^{13}C -depleted compared to the dead leaves and soil detritus of *S. sabulicola*. Compared to the litter and detritus of *S. sabulicola*, the plant litter (dead stem) of *A. horridus* ($\delta^{15}\text{N} = 4.2 \pm 1.6\text{‰}$) and soil detritus under *A. horridus* ($\delta^{15}\text{N} = 3.7 \pm 0.2\text{‰}$) were ^{15}N -enriched.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of invertebrates

A subset of the above-mentioned above- and belowground invertebrates were included in the stable isotope analysis for the construction of FPO trophic structure (Figure 1). Aboveground, invertebrates that have $\delta^{13}\text{C}$ values close to the dead leaves of *S. sabulicola* ($\delta^{13}\text{C} = -14.0 \pm 0.6\text{‰}$) include the saprophilous and fungivorous *Zygoribatula* sp. ($\delta^{13}\text{C} = -14.7 \pm 0.7\text{‰}$), sap feeders *Deltocephalinae* sp. ($\delta^{13}\text{C} = -13.9 \pm 0.4\text{‰}$) and Diapsididae sp. ($\delta^{13}\text{C} = -15.7 \pm 0.8\text{‰}$). Saprophilous and fungivorous *Liposcelis* sp. was markedly ^{13}C -depleted ($\delta^{13}\text{C} = -20.6 \pm 3.3\text{‰}$) compared to the fresh leaves of *S. sabulicola* ($\delta^{13}\text{C} = -15.1 \pm 0.7\text{‰}$). Similarly, the herbivores *Sibinia* sp. ($\delta^{13}\text{C} = -21.0 \pm 1.6\text{‰}$) and *Haplothrips* sp. ($\delta^{13}\text{C} = -17.8 \pm 1.9\text{‰}$) were ^{13}C -depleted compared to the fresh leaves of *S. sabulicola*. Dune surface dwellers were also ^{13}C -depleted compared to the dead leaves of *S. sabulicola* including *C. detritus*: $\delta^{13}\text{C} = -15.8 \pm 1.8\text{‰}$, *O. laeviceps*: $\delta^{13}\text{C} = -16.0 \pm 1.5\text{‰}$, and *O. plana*: $\delta^{13}\text{C} = -17.2 \pm 2.0\text{‰}$, while the $\delta^{13}\text{C}$ values of *P. globosa* were markedly depleted ($\delta^{13}\text{C} = -25.2 \pm 0.6\text{‰}$) compared to the tenebrionid beetles from the genus *Onymacris*.

Predators *Salticinae* sp. ($\delta^{13}\text{C} = -14.1 \pm 0.3\text{‰}$) and parasitoids *Haltichellinae* sp. ($\delta^{13}\text{C} = -14.0 \pm 0.3\text{‰}$) had $\delta^{13}\text{C}$ values almost identical to the dead leaves of *S. sabulicola* ($\delta^{13}\text{C} = -14.0 \pm 0.6\text{‰}$). Scale insects predator *Cybocephalus* sp. ($\delta^{13}\text{C} = -13.5 \pm 0.2\text{‰}$) and predator *Thysanina* sp. ($\delta^{13}\text{C} = -12.8\text{‰}$) was 0.5-1.2 ‰ ^{13}C -enriched compared to the same plant material. In contrast, the $\delta^{13}\text{C}$ value of *Nanolpium* sp. ($\delta^{13}\text{C} = -18.4 \pm 2.5\text{‰}$) was markedly ^{13}C -depleted compared to the dead leaves of *S. sabulicola* as well as other predatory species. The summary of aboveground invertebrates, their expected trophic feeding types, and isotopic values are summarised in Table 2. Belowground, both bacterial- ($\delta^{13}\text{C} = -24.6 \pm 1.9\text{‰}$) and fungal-feeding nematodes ($\delta^{13}\text{C} = -23.6 \pm 0.2\text{‰}$) were markedly ^{13}C -depleted compared to dead leaves of *S. sabulicola*.

Values of $\delta^{15}\text{N}$ in a consumer's tissue are more ^{15}N -enriched compared to those of its diet, and this is termed "enrichment" as denoted by Δ , where $\Delta^{15}\text{N} = \delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{diet}}$ (Eq. 1). In the present study, $\Delta^{15}\text{N}$ values were used to calculate trophic positions (TP) of above- and belowground invertebrates at the *S. sabulicola* FPOs, where dead leaves of the fog plant were assumed to form the trophic base ($\Delta^{15}\text{N} = 0$) of the invertebrate food web. Calculation of trophic positions assumes the enrichment factor per trophic level equals 3.4‰ according to a previous large-scale study on marine and freshwater organisms by Minagawa & Wada (1984). Therefore, Eq. 1 is rewritten as $\text{TP} = [\delta^{15}\text{N}_{\text{invertebrate}} - \delta^{15}\text{N}_{\text{baseline}}] / 3.4$, where $\delta^{15}\text{N}_{\text{invertebrate}} = \delta^{15}\text{N}$ values of above- and belowground invertebrates found

on or within proximity to *S. sabulicola*, and $\delta^{15}\text{N}_{\text{baseline}}$ = dead leaves of *S. sabulicola*. Likewise, the $\delta^{15}\text{N}_{\text{baseline}}$ to calculate the trophic position of *H. zigzagus*, the herbivore species found feeding on *A. horridus*, was assumed to be the $\delta^{15}\text{N}$ values of dead *A. horridus* stem.

Overall, the gradient spanned over 16 δ units in $\Delta^{15}\text{N}$ values for all FPO invertebrates that occupied 5 trophic positions. The first trophic position was occupied by primary decomposers including *Zygoribatula* sp. ($\Delta^{15}\text{N} = 0.05 \pm 0.6\text{‰}$) and *Liposcelis* sp. ($\Delta^{15}\text{N} = 2.8 \pm 1.9\text{‰}$) as well as sap feeder *Diapsididae* sp. ($\Delta^{15}\text{N} = 0.9 \pm 0.6\text{‰}$). The second trophic level was occupied by the most taxa with various feeding strategies, including sap feeder *Daltocephalinae* sp. ($\Delta^{15}\text{N} = 3.2 \pm 1.2\text{‰}$), predators *Thysanina* sp. ($\Delta^{15}\text{N} = 4.0\text{‰}$), *Nanolpium* sp. ($\Delta^{15}\text{N} = 5.5 \pm 0.7\text{‰}$), and *Cybocephalus* sp. ($\Delta^{15}\text{N} = 5.9 \pm 2.8\text{‰}$), bacterial-feeding nematodes ($\Delta^{15}\text{N} = 5.4 \pm 1.2\text{‰}$), as well as herbivore *H. zigzagus* ($\Delta^{15}\text{N} = 6.2 \pm 1.1\text{‰}$), and honeydew feeder *C. detritus* ($\Delta^{15}\text{N} = 6.6 \pm 0.9\text{‰}$). Both tenebrionid species occupied the third trophic level: *O. laeviceps* ($\Delta^{15}\text{N} = 6.7 \pm 5.0\text{‰}$) and *O. plana* ($\Delta^{15}\text{N} = 7.2 \pm 1.8\text{‰}$). *P. globosa* is excluded from trophic level calculation because of their distinctive $\delta^{13}\text{C}$ values and lack of a suitable baseline value. The fourth trophic level was occupied by *Salticinae* sp. ($\Delta^{15}\text{N} = 10.9 \pm 0.9\text{‰}$) and *Haplothrips* sp. ($\Delta^{15}\text{N} = 11.4 \pm 2.5\text{‰}$), while *Sibinia* sp. ($\Delta^{15}\text{N} = 13.7 \pm 1.4\text{‰}$) and *Haltichellinae* sp. ($\Delta^{15}\text{N} = 16.7 \pm 0.4\text{‰}$) occupied the fifth trophic level. Fungal-feeding nematodes were positioned way below the trophic baseline due to their markedly low $\Delta^{15}\text{N}$ value ($-11.04 \pm 3.90\text{‰}$).

Diet estimates of FPO invertebrates

Estimates for the diet of aboveground invertebrates were conducted using the Stable Isotope Mixing Models (function “simmr”) (Govan et al., 2023). The analyses were based on both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers (mixtures) as well as their potential diets (sources). Corrections were considered for the analyses, which included the standard deviations for consumers’ $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, the % of carbon and nitrogen of diet, as well as enrichment factors for $^{13}\text{C} = 0.4 \pm 1.3\text{‰}$ and $^{15}\text{N} = 3.4 \pm 1.0\text{‰}$ according to Post (2002). Mixing models were used to estimate i) the contributions of dead leaf, soil detritus, and scale insects (*Diapsididae* sp.) to the diet of primary as well as secondary decomposers and ii) the contributions of lower ranked invertebrates to the diet of predatory taxa.

Estimations of potential dietary components of the sampled invertebrates varied markedly as indicated by high standard deviations (Table 3 and Table 4). Nevertheless, the estimates suggested that fungal-infected dead leaves of *S. sabulicola* constituted a large proportion in the diet of *Zygoribatula* sp. ($78 \pm 27\%$) and *Cybocephalus* sp. ($67 \pm 17\%$). Soft scales *Diapsididae* sp. had substantial contributions to the diets of *Liposcelis* sp. ($73 \pm 42\%$), *O. laeviceps* ($78 \pm 19\%$), and *O. plana* ($89 \pm 5\%$). Soil detritus which comprised of light fraction organic matter under *S. sabulicola* FPOs showed an important contribution to the diet of *C. detritus* ($86 \pm 18\%$). Among predatory taxa that occupy lower trophic levels (TL), *Liposcelis* sp. contributed $65 \pm 10\%$ to the diet of *Nanolpium* sp. (TL = 2) while *Zygoribatula* sp. contributed $46 \pm 31\%$ to the diet of *Thysanina* sp. (TL = 2). Among the “higher” predatory taxa, *Cybocephalus* sp. contributed $37 \pm 17\%$ to the diet of *Salticinae* sp. (TL = 4) while *Haplothrips* sp. contributed $75 \pm 10\%$ to the diet of *Haltichellinae* sp. (TL = 5). The summary of the trophic relationships was shown in Figure 3.

Discussion

The ability of *S. sabulicola* to establish itself in barren environments from the seedling stage classifies it as a pioneer species. However, unlike most pioneer species which were eventually replaced by other successional species once stable conditions are achieved, *S. sabulicola* continues to grow into large grass tussocks with hummock formations and ultimately become the climax species. The persistence of *S. sabulicola* as the only plant species on the higher dunes can be attributed to two main mechanisms. Firstly, the fog plant possesses distinctive morphology that enables it to harvest fog and exploit near-surface moisture effectively, as well as to anchor itself on the highly unstable sand dunes (Ebner et al., 2011; Louw & Seely, 1980; Roth-Nebelsick et al., 2012). Secondly, abiotic factors such as the rapid sand movement on the dunes and scarce rainfall hinder the succession of the fog and dune specialists by other plant species (Yeaton, 1988). Overall, the unusual formation of *S. sabulicola* FPOs highlights their potential as habitats for various invertebrates and a unique food web.

In this study, we illustrated that *S. sabulicola* FPOs harbor trophic niches for a diverse array of above- and belowground invertebrates. Aboveground through bush-beating, we found a total of 12 arthropod taxa on the leaf surface and within the leaf sheaths, with an additional 7 taxa observed, but not studied in detail. In contrast, flotation of soil samples yielded only a few soil microarthropod species which were predominantly mites. Belowground microarthropods under *S. sabulicola* hummock were previously recognized by

Coineau & Seely (1983). They retrieved a higher diversity of taxa than us, especially with the findings of *Arthropleona* springtails (a single cuticle found by us). Their sampling methodology differed from ours, as they frequently watered a well in the sand for one week before sampling 10 L of sands. Our sampling design was likely not sensitive enough to capture the rare taxa (Pauropoda). From the cuticle we found, we suspect the reported *Arthropleona* to belong to a rather common, yet undescribed, Entomobryidae we observed in the Kuiseb and in Gobabeb. The species is a rapid runner that could have rapidly aggregated in the watered well while being scarce in the natural conditions targeted by our sampling. Though bush-beating and soil sampling are difficult to compare, arthropod species richness and biomass were evidently higher on the grass canopy of *S. sabulicola* than in the sand near the roots, revealing the complexity of these “hidden oases”. Soil life is probably inhibited by the instability of the dune surface (Scholz, 1972), but the presence of a thriving fauna community on the aboveground canopy was undeniably enabled by an ample supply of fog water stored in the grooved stems of *S. sabulicola* (Ebner et al., 2011). Sufficient wetting of aboveground litter has also been previously observed to undergo rapid fungal decomposition which additionally provides aboveground fauna with high-quality litter (K. Jacobson et al., 2015). Overall, the presence of moisture, food sources, and potential wind and solar protection provided by the grass tussock canopy collectively render it a suitable habitat for the discovered invertebrates.

Among the aboveground soil invertebrates that have similar $\delta^{13}\text{C}$ values as *S. sabulicola*, their trophic levels were observed to span from the detritivore (*Zygoribatula* sp.) to the predatory taxa (*Cybocephalus* sp. to *Salticinae* sp., and *Haltichellinae* sp.). This points to *S. sabulicola* as the primary source of carbon that fuelled the aboveground FPO food web from the bottom to the higher trophic levels (Figure 2, Figure 3). However, the $\delta^{13}\text{C}$ values of the other half of the FPO invertebrates were found to be ^{13}C -depleted, some markedly, compared to the litter of *S. sabulicola*. For instance, *Liposcelis* sp. was about 6‰ depleted compared to the litter of *S. sabulicola*. However, it is not clear if the markedly depleted $\delta^{13}\text{C}$ values of this saprophilous and fungivorous species mirrored the plant sap of *S. Sabulicola*, since $\delta^{13}\text{C}$ values of phloem sap have been previously reported to be like plant leaves (Sagers & Goggin, 2007). Depleted $\delta^{13}\text{C}$ values compared to *S. sabulicola* were also apparent in *Haplothrips* sp. and *Sibinia* sp., both typically classified as plant herbivores. Moreover, the phenomenon of markedly depleted $\delta^{13}\text{C}$ values among plant herbivores seemed to occur only within the FPO soil food web, whereas *H. zigzagus*, the arthropod that fed on the stem of *A. horridus*, showed a 3‰ enrichment in $\delta^{13}\text{C}$ compared to its host plant.

As mentioned above, the markedly depleted $\delta^{13}\text{C}$ values of some of the plant herbivores of the FPOs differed from earlier studies that reported a trend of increasing $\delta^{13}\text{C}$ values moving up the trophic level (Ponsard & Arditi, 2000; Scheu & Falca, 2000). Past research has reported variations in $\delta^{13}\text{C}$ values of different primary and secondary photosynthetic products from various temperate plants e.g. ^{13}C -enriched sucrose and starch and ^{13}C -depleted lignin and lipid (Gleixner et al., 1993). Therefore, these herbivore species yet with distinct $\delta^{13}\text{C}$ values compared to their host plant may be feeding on specific types of photosynthetic products with depleted $\delta^{13}\text{C}$ values than the bulk leaves or litter of *S. sabulicola*. Apart from diet, the lower $\delta^{13}\text{C}$ values could also be explained by higher lipid content in animal tissues, which is generally more ^{13}C -depleted compared to proteins and carbohydrates. The depleted $\delta^{13}\text{C}$ values due to higher lipid content are shown by negative correlations between invertebrate C/N ratios and their $\delta^{13}\text{C}$ values (Focken & Becker, 1998; Post et al., 2007). Overall, we found significant negative correlations between the $\delta^{13}\text{C}$ values of *Liposcelis* sp. and their C/N ratios (adjusted R-squared = 0.93, p-value = <0.001) which supports this hypothesis, but no correlation between $\delta^{13}\text{C}$ values and C/N ratios were found for *Haplothrips* sp. and *Sibinia* sp. Additionally, we discovered that the FPO invertebrates showed a pattern of lower C/N ratios (Table 2) compared to soil invertebrates from temperate forests and grasslands (Crotty et al., 2014; Ponsard & Arditi, 2000). This finding suggests that climatic influence, in this case hyperaridity, may be driving these differences. This hypothesis is supported by prior studies which demonstrated that lipid storage plasticity is associated with starvation tolerance in arthropods under temperature manipulations (Jensen et al., 2018; van Dooremalen & Ellers, 2010).

Given the importance of detritivores in the decomposition of plant litter outside of rain events in the Namib Desert (K. Jacobson et al., 2015; K. M. Jacobson & Jacobson, 1998), we further focused on the diet of detritivore species at FPOs. In the present study, we found oribatid mites from the genus *Zygoribatula* sp. to be the most abundant primary decomposer species inhabiting the leaves of *S. sabulicola*. Previous studies have reported that oribatid mites from the same genus, *Zygoribatula exilis*, exclusively occupy trees or lichens (Fischer et al., 2010). Isotope data from prior studies on *Z. exilis* in temperate forests indicated a slight ^{15}N -enrichment relative to the tree barks, implying that they feed on algae and bryophyte (Erdmann et al., 2007). Similarly, our diet estimates showed a majority contribution of dead leaves with heavy fungal infection to the diets of *Zygoribatula* sp., thus highlighting their importance as the main primary decomposer of the *S. sabulicola* FPOs and potentially helping to control fungal pathogens of the fog plant.

We further investigated the roles of tenebrionid beetles and dune ants as potentially important detritivores of the *S. sabulicola* FPOs. Our stable isotope data confirmed the niche separation between *P. globosa* and other tenebrionid beetles from the genus *Onymacris* (Figure 2). In agreement with previous studies, we showed that specimens from the genus *Onymacris* tend to inhabit open sand and vegetation-less dune slips compared to *P. globosa* which occupies the dry riverbeds and the gravel plains (Osberg et al., 1986; Roberts et al., 1991). In terms of diets, our estimates showed that the leaf litter of *S. sabulicola* did not have significant contributions as food resources for *O. laeviceps* and *O. plana*. Furthermore, the tenebrionid beetles also occupy a rather high trophic level like other predators. Previously, wind-blown litter has been suggested to dominate the diet of these species (Holm & Edney, 1973), but our stable isotope data provide evidence that plant litter plays a less important role in their diets compared to other food sources with higher $\delta^{15}\text{N}$ values, such as a diet rich in animal-derived sources. The dune ants *C. detritus*, while proficient at clearing surface detritus, do not function as detritus consumers themselves (Curtis, 1985a). Instead, they primarily subsist on a diet of honeydews, which are secreted by aphids and scale insects (Curtis, 1985b). In line with this, we observed that the $\delta^{13}\text{C}$ values of *C. detritus* closely mirrored those of the Diaspididae sp. that were notably abundant within the inner sheath of *S. sabulicola*. However, diet estimates also showed a high contribution of soil detritus in the diet of *C. detritus*, confirming the large diet spectrum of this generalist feeder. In summary, these results indicate that *O. laeviceps*, *O. plana*, and *C. detritus* were not the main consumers of *S. sabulicola*'s litter, and likely played a smaller role than *Zygoribatula* sp. in the decomposition of plant litter within the FPOs.

Belowground, soil nematodes were predominantly bacterial feeders (bacterivores) followed by fungal feeders (fungivores), which mirrors their trophic composition of the well-studied gravel plains nearby and other arid ecosystems (Marais et al., 2020; Pen-Mouratov et al., 2004; Steinberger Y. et al., 1988; Treonis et al., 2022). Overall, the markedly depleted $\delta^{13}\text{C}$ values of both trophic groups of nematodes compared to the litter of *S. sabulicola* suggest that the fog plant might not be their main carbon source. Compared to the $\delta^{13}\text{C}$ values of aboveground invertebrates which in general resemble $\delta^{13}\text{C}$ values of *S. Sabulicola*, the $\delta^{13}\text{C}$ values of belowground fauna indicate that their main energy source originated from wind-blown sediments. The distinct energy sources between the above- and the belowground food web suggest two separate niches. According to their ^{15}N -enrichment ($\Delta^{15}\text{N}$), bacterivores occupied the second trophic level of the FPO food web, confirming their trophic roles as secondary decomposers (Kudrin et al., 2015; Melody et al., 2016). Markedly depleted $\Delta^{15}\text{N}$ values, however, positioned the fungivorous nematodes way below the baseline of the *S. sabulicola* plant tissues, showing similar values as lichen-feeding oribatid mites in a temperate forest (Erdmann et al., 2007). To the best of our knowledge, there is no other in-situ comparison of $\delta^{15}\text{N}$ values among fungal-feeding nematodes in the current literature. Results from a feeding experiment conducted by Ruess et al. (2004) showed that the depleted $\Delta^{15}\text{N}$ of fungivores *Aphelenchoides saprophilus* originated from its fungal food source that was depleted in $\Delta^{15}\text{N}$ compared to the medium where the fungi grew. Together with these previous findings, our results indicate that depleted $\Delta^{15}\text{N}$ of fungivores may be related to feeding on low-quality food sources such as blown-in detritus, lichens, or fungal biomass which is typically N-depleted (Mouginot et al., 2014), as well as mechanisms of ^{15}N fractionations by nematode to compensate for low-quality food resources.

Methods

Site description

The study was conducted in the Namib Sand Sea near the Gobabeb Namib Research Institute (23°34'S, 15°03' E, 407m a.s.l., ~1km south across the Kuiseb River). *S. sabulicola* is the dominant plant species growing on the Aeolian dunes, particularly the plinth (flattened slope on the dune base) and the windward slopes (Robinsonj & Seely, 1980; Southgate et al., 1996). At the dune base, *S. sabulicola* was found to coexist with other *Stipagrostis* species, *Acanthosicyos horridus* (!Nara melon) and *Cladoraphis spinosa*. A total of seven FPOs established by *S. sabulicola* with two contrasting grass tussock sizes (3 young and 7 mature tussocks with signs of senescence) were selected as study sites. Mature and young FPOs referred to growth stages of *S. sabulicola* that forms the FPO. At mature FPOs, sizable sand hummocks (up to 10m x 9m wide) were formed by tussocks that frequently grow up to 2 meters tall, while young plants (under 1 meter in height) did not accumulate visible hummocks yet. Open sand next to the FPOs were assigned as controls. All three young FPOs and two mature FPOs were located on dune ridges, while two mature FPOs were located on the windward plinth and dune base respectively.

Sampling and processing of samples

Field work and sampling of all study materials were carried out during the fog season in early September 2022. Samples for extracting soil nematodes and other belowground invertebrates consisted of two replicates (one for wet extractions for nematodes and one for

other fauna) of 3-4 soil cores each per FPO (diameter 5cm, height 5cm), with 84 samples in total. Immediately after sampling, nematodes were extracted from soil samples using a modified Baermann method (wet extraction) for 48 hours. In this study, we used "soil" as a generic term for "ground substrate", which in this case refers to sandy substrate from the dunes. At the end of the extraction, nematodes were heat-killed and fixed with formaldehyde. The nematodes were identified to genus level, and where possible to species, under an inverted microscope (400x magnification). The body length and width of each specimen was measured and translated into body mass using the formula of Andrassy (1956). Nematode genera were assigned to bacterivorous, fungivorous, and omnivorous feeding types following Yeates et al. (1993). Several adults from each genus were isolated for preparation on permanent slides and species determination. The remaining bacterivores yielded sufficient biomass for isotope analysis, hence were hand picked under the inverted microscope in two samples, which weighed 48.5 and 105.8 µg dried nematode mass, respectively. The numbers and biomass of fungivorous nematodes did not suffice, thus two samples containing both bacterivores and fungivores were weighed together. Since in both of these pooled samples, the biomass ratios of the two trophic groups (m_{bac} and m_{fun}) were accurately measured, and the isotopic signal for bacterivores (F_{bac}) was already determined, the isotope signals (F_{fun}) could be calculated from the isotopic signal F_{pool} and biomass m_{pool} of the pooled samples, using a two pools mass-balance equation: $m_{pool}F_{pool} = m_{bac}F_{bac} + m_{fun}F_{fun}$, where m = the biomass ratios and F = the fractional isotopic abundance of bacterivorous and fungivorous nematodes within the two pooled samples.

Other soil arthropods were extracted using a combination of Berlese-Tullgren (dry extraction), underground pitfalls, and flotation methods. Bush-beating was used to sample the small invertebrates living on the plant, while macrofauna (ants and darkling beetles) were collected on sight by hand. Stems of the plant were also peeled under the stereomicroscope to recover small invertebrates living under the leaf layers. All fauna except for nematodes were killed and preserved in 100% ethanol solution. Preservation of faunas in ethanol and formalin can affect their isotopic values but the shift in values was usually less than 1‰ (Fábán, 1997; Krab et al., 2012; Sticht et al., 2006). Plant materials (fresh leaves, dead leaves, plant roots, and rhizosheath) were dried at 60°C for 3-5 days. Soil detritus was extracted using a flotation method (3:1 water:soil ratios) then filtered through a fine mesh (6 µm).

Above ground invertebrates were collected by beating the stems and leaves of the grass into a plastic box, then captured with a mouth aspirator modified for immediate preservation in 100% ethanol. We collected most arthropods that did not fly away immediately. We sorted the animals into morphospecies using a stereo-microscope. We selected the morphospecies we estimated to offer enough biomass for stable isotopes analysis and molecular sequencing. One individual of each was selected for genome skimming, either from a cutted leg, or from the whole individual depending on the size. DNA extractions were done using the DNeasy Blood & Tissue Kit (Qiagen, Hilden), Illumina libraries were made using the NEBNext® Ultra™ II DNA Library Prep Kit (New England Biolabs, Ipswich), for a 150 bp insert size. Sequencing was done at Novogene UK on a NovaSeq 6000 system (Illumina, San Diego), aiming for 10Gb per library. The sequenced libraries were trimmed with Trimmomatic (v0.39) (Bolger et al., 2014) then assembled with SPAdes (v3.14.1) (Bankevich et al., 2012). The COI-5P marker (658 bp) and the 28S rDNA full gene was searched directly in the scaffolds using Blastn (v2.13.0+). The integrity of the protein coding sequences was verified, and each sequence was first queried on Genbank to check for obvious contaminants. We further confirmed that none of the sequences could be directly assigned to a species using the BOLD identification tool. We then proceeded to a phylogenetic placement. We adapted our method case by case, but the general approach was as follows. For each morphospecies, we subselected the BOLD public database using the lowest taxonomic group we recognized (Araneae, Cicadellidae, Coccoidea, Cucujoidea, Hymenoptera, Psocodea, Pseudoscorpionides and Thysanoptera). For each supra-family taxa selection, we sampled the database allowing from 20 to 50 records for each family (duplicated sequences removed, records randomly selected, and number of maximum records manually tuned to keep the number of OTUs around or below 3000). A rapid phylogenetic placement was performed using MAGUS (Smirnov & Warnow, 2021) for multiple sequence alignments and FastTree2 (Price et al., 2010) for ML tree inference. When the dataset contained less than 400 OTUs, we used Muscle v5 (Edgar, 2022) + Raxml-ng (Kozlov et al., 2019) instead. The trees were visualised using iTOL (Letunic & Bork, 2021). The closest family was selected as a novel filter of the BOLD database, and the sampling process was repeated at genus level. For some taxa, COI-5P did not allow a taxonomic placement. In such cases we retrieved suitable comprehensive phylogenetic datasets based on 28S rDNA and used them to accurately confirm the family of the concerned species. Then again, high resolution placement was done using the COI-5P against the BOLD public database. Once the closest genus could be identified, we searched the literature for previous reports in Namibia. Details for each species are provided in Appendix 1.

Stable isotope analysis and statistics

Prior to weighing, all plant and detritus samples were hand-milled manually using a pestle and mortar to ensure homogeneity and transferred into tin capsules. Invertebrates were transferred directly in tin capsules and oven-dried at 60°C for at least 24 hours. Nematodes were weighed in tin capsules with lids to avoid biomass loss from evaporation. Bigger arthropods (tenebrionid and blister beetles) were freeze-dried (Heto PowerDry LL3000; Thermo Fisher Scientific, Waltham, USA) for 48-72 hours. C/N concentrations and stable isotopes were quantified using an elemental analyzer coupled to isotope-ratio mass spectrometer (IRMS) (MAT 251, Finnigan, Bremen, Germany) (Langel & Dyckmans, 2014). Isotope ratios of all samples were reported in conventional δ -notation: , where R is the ratio of heavier to lighter isotope. The δ values were expressed as per mill (‰) or parts per thousand.

All statistical analyses were conducted in R version 3.3.2 (R Core Team, 2020). The R package Stable Isotope Mixing Models (function “*simmr*”) was used for the reconstruction of faunal diet (Govan et al., 2023). The mixing models required both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers as well as likely sources (diet) including corrections (i.e. standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, enrichment factor for $^{13}\text{C}=0.4\pm1.3\text{‰}$ and $^{15}\text{N}=3.4\pm1.0\text{‰}$ according to, as well as the % of carbon and nitrogen in diet). *Simmr* was used to estimate: 1) the contributions of dead leaf, soil detritus, and scale insects to the diets of detritivore species and ii) the contributions of invertebrates from lower trophic levels to the diet of predatory species. Fitting linear models (function “*lm*”) was used to determine the correlation between $\delta^{13}\text{C}$ of invertebrates and their C/N ratios.

Plant Collection Statement

The plant collection and use were in accordance with all the relevant guidelines provided by the Namibian National Commission on Research, Science, and Technology, as stipulated on the research permit issued with Permit Number RPIV00672022. The plant material used in this study was identified by Dr. Tatiana Miranda and Dr. Martin Ebner, both co-authors of this paper. They have previously published a paper on the same plant *S. sabulicola* (Ebner et al., 2011).

Data deposition

Upon acceptance of the manuscript, the animals DNA sequences will be publicly deposited on BOLD (<https://www.boldsystems.org>) and voucher specimens will be deposited in the collections of the National Museum of Namibia, Windhoek. All identifiers and accession numbers are to be provided in the final version.

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Tables

Table 1 Total carbon, total nitrogen, C/N ratios, and isotopic values of basal resources. Values are reported as mean $\pm$ SD.

samples	n	Total carbon (%)	Total nitrogen (%)	C/N ratio	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
1. <i>Stipagrostis sabulicola</i>						
Fresh leaves	5	45.5±1.3	1.4±0.3	34.9±10.4	-15.1±0.7	0.2±1.5
Dead leaves	7	43.0±3.0	0.5±0.1	88.5±20.4	-14.0±0.6	-1.9±1.6
Dead leaves with fungal infection	12	43.8±2.3	0.9±0.5	57.0±23.1	-14.0±0.5	-0.7±2.5
Root	6	45.8±0.5	0.6±0.1	71.8±10.1	-14.1±0.3	0.1±1.4
Rhizosheath	8	20.4±6.7	0.5±0.2	43.5±5.6	-13.7±0.4	0.8±0.4
Soil detritus	7	34.5±9.8	0.9±0.2	38.8±11.3	-14.3±0.2	2.0±1.2
2. <i>Acanthosicyos horridus</i>						
Litter (Dead stem)	8	43.3±3.1	1.6±0.9	38.2±27.6	-21.7±0.8	4.2±1.6
Soil detritus	6	28.8±6.6	1.1±0.2	27.5±9.3	-17.1±1.2	3.7±0.2

Table 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values found for the aboveground invertebrates of *S. sabulicola* FPOs. The feeding habits expected from the known biology of each group were indicated

Taxon	n	Expected feeding habit	Source	$\delta^{13}\text{C}$	$\Delta^{15}\text{N}$	C/N
<i>Zygoribatula</i> sp.	5 (pooled)	Saprophilous, fungivorous	(Erdmann et al., 2007)	-14.7±0.7‰	0.05±0.6‰	5.2±0.3
<i>Diapsididae</i> sp.	5 (pooled)	Sap feeder	(Curtis, 1985a)	-15.7±0.8‰	0.9±0.6‰	7.7±1.2
<i>Liposcelis</i> sp.	9	Saprophilous, fungivorous	(Wondale Endshaw & Berhanu Hiruy, 2020)	-20.6±3.3‰	2.8±1.9‰	9.8±4.7
<i>Deltocephalinae</i> sp.	3	Sap feeder	(Dmitriev, 2001)	-13.9±0.4‰	3.2±1.2‰	3.8±0.1
<i>Thysanina</i> sp.	1	Predator	(Lyle & Haddad, 1938)	-12.8‰	4.0‰	3.4
<i>Nanolpium</i> sp.	4	Predator	(Judson & Heurtault, n.d.)	-18.4±2.5‰	5.5±0.7‰	5.9±1.3
<i>Cybocephalus</i> sp.	4	Scale insect's predator	(Smith, 2022)	-13.5±0.2‰	5.9±2.8‰	4.6±0.3
<i>Camponotus detritus</i>	6	Mainly honeydew feeder	(Curtis, 1985b)	-15.8±1.8	6.6±0.9‰	4.2±0.3
<i>Onymacris laeviceps</i>	3	Omnivorous, mainly on plant detritus but also on green plants and dead animals	(Holm & Edney, 1973)	-16.0±1.5	6.7±5.0‰	4.7±1.1
<i>Onymacris plana</i>	4	Omnivorous, mainly on plant detritus but also on green plants and dead animals	(Holm & Edney, 1973)	-17.2±2.0	7.2±1.8‰	5.0±0.3
<i>Physadesmia globosa</i>	3	No specific diet, probably omnivorous	(Wharton & Seely, 1982)	-25.2±0.6	8.5±1.6‰	5.3±0.7
<i>Salticinae</i> sp.	2	Predator	(Haddad & Wesolowska, 2011)	-14.1±0.3‰	10.9±0.9‰	3.5±0.1
<i>Haplothrips</i> sp.	6	Herbivorous, pollinizer	(Wang et al., 2022)	-17.8±1.9‰	11.4±2.5‰	4.9±0.6
<i>Sibinia</i> sp.	5	Herbivorous	(Henschel et al., 2003)	-21.0±1.6‰	13.7±1.4‰	4.7±0.1
<i>Haltichellinae</i> sp.	2	Carnivorous during larval development then nectar or honeydew feeder.	(Heraty et al., 2013)	-14.0±0.3‰	16.7±0.4‰	3.8±0.1

Table 3 Diet estimations of detritivores by stable isotope mixing models (mean % ±SD). Mean values above 15% are marked by bold letters

	<i>C. detritus</i>		<i>Cybocephalus</i> sp.		<i>Liposcelis</i> sp.		<i>O. laeviceps</i>		<i>O. plana</i>		<i>Zygoribatula</i> sp.	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Dead leaves	0.034	0.027	0.124	0.095	0.252	0.422	0.059	0.046	0.034	0.026	0.079	0.133
Fungal-infected dead leaves	0.033	0.026	0.668	0.169	0.007	0.005	0.095	0.189	0.032	0.023	0.799	0.273
Soil detritus	0.856	0.179	0.174	0.156	0.009	0.007	0.063	0.050	0.041	0.032	0.034	0.027
Softscale insect (<i>Diaspididae</i> sp.)	0.077	0.165	0.034	0.024	0.732	0.420	0.782	0.189	0.893	0.050	0.089	0.225

Table 4 Diet proportions of predators estimated by stable isotope mixing models (mean % $\pm$ SD). Mean values above 15% are marked by bold letters.

	<i>Nanolpium</i> sp.		<i>Thysanina</i> sp.		<i>Salticinae</i> sp.		<i>Haltichellinae</i> sp.	
	mean	SD	mean	SD	mean	SD	mean	SD
<i>Liposcelis</i> sp.	0.650	0.100	0.056	0.086	0.061	0.048	0.034	0.028
<i>Diaspididae</i> sp.	0.090	0.078	0.081	0.116	0.088	0.068	0.040	0.033
<i>Deltocephalinae</i> sp.	0.055	0.046	0.149	0.216	0.120	0.100	0.036	0.028
<i>Zygoribatula</i> sp.	0.119	0.085	0.464	0.307	0.078	0.058	0.033	0.025
<i>Sibinia</i> sp.	0.023	0.014	0.026	0.019	0.095	0.058	0.047	0.041
<i>Cybocephalus</i> sp.	0.037	0.029	0.190	0.252	0.366	0.166	0.059	0.077
<i>Haplothrips</i> sp.	0.026	0.017	0.033	0.027	0.192	0.133	0.750	0.103

Figures

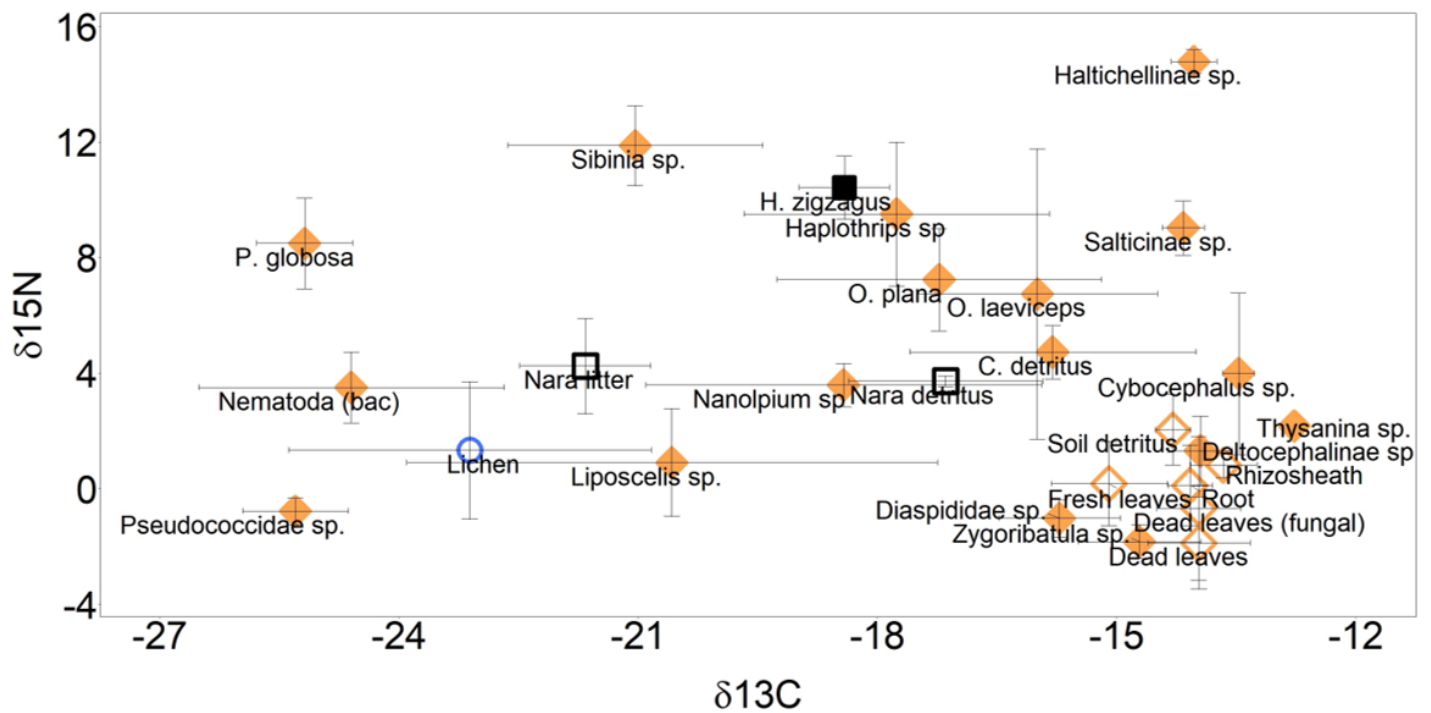


Figure 1

Mean ($\pm$ SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of different basal resources (void shapes) and invertebrates (filled shapes) associated with different basal resources according to different colour and shapes: sand diamonds (*S. sabulicola*), black squares (*A. horridus*), and blue circle (hypolithic biomass).

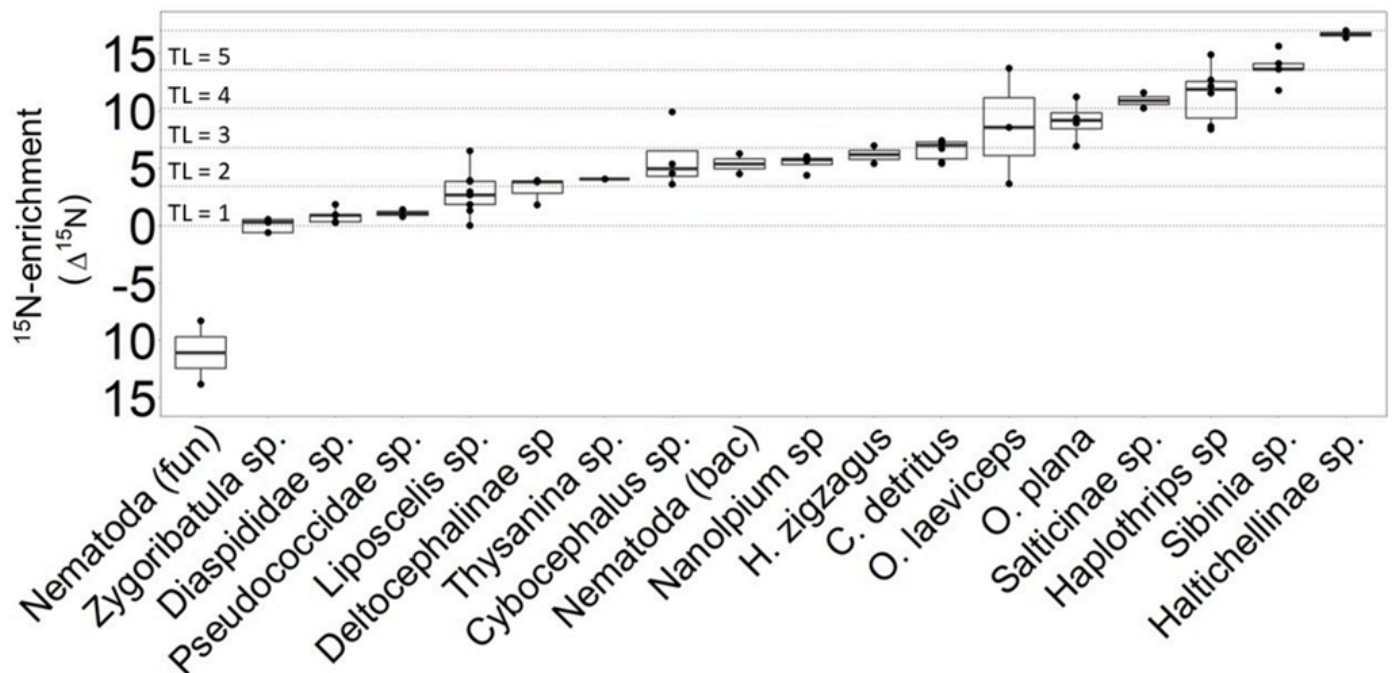


Figure 2

^{15}N -enrichment of all above- and belowground invertebrates sampled from *S. sabulicola* FPOs as well as one species (*H. zigzagus*) from *A. horridus* signatures. TL = trophic level based on an enrichment factor of $\delta^{15}\text{N}=3.4\text{‰}$ per trophic level.

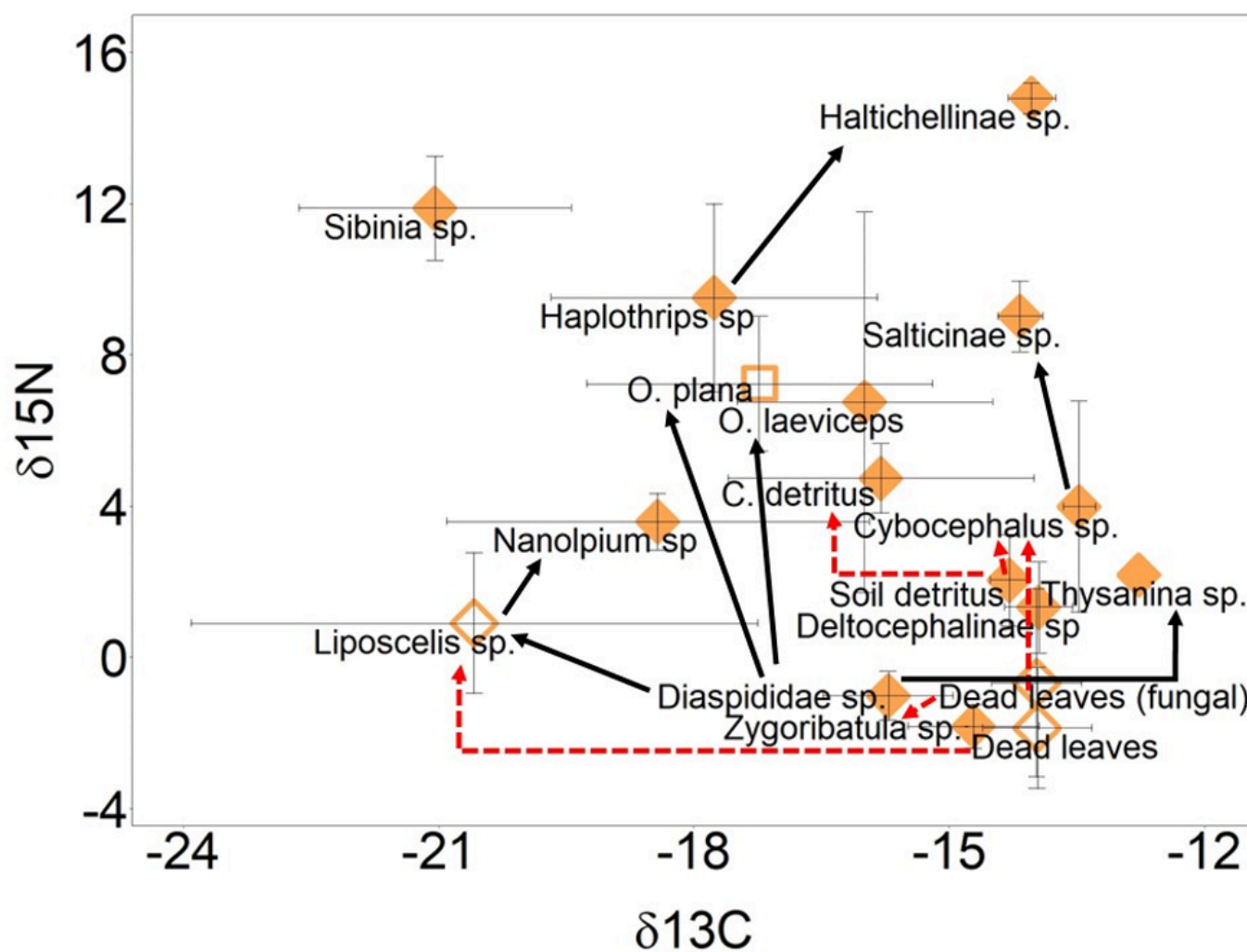


Figure 3

Summary of detritus and predatory food web according to stable isotope mixing models. Dotted red arrows indicate the detrital pathway while solid black arrows indicate predation.

Supplementary Files

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