

# Collapse of trophic-niche structure in belowground communities under anthropogenic disturbance

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**Abstract.** The niche concept is a central paradigm in ecology, but empirical evidence on how the niche structure of belowground communities is affected by ecosystem disturbance is lacking. Niche differentiation evolves due to stable coexistence of species in a community, suggesting that in unstable communities, the niches of species should largely overlap. Here, we test this prediction using empirical data on the trophic-niche structure of several belowground collembolan communities of natural (forest and meadow) and disturbed (pasture and urban lawn) habitats. Scaled stable isotope compositions of carbon and nitrogen were used to reveal the trophic specialization of species. In full agreement with the theoretical predictions, trophic-niche structure collapsed in disturbed habitats, which was illustrated by decreased interspecific and increased intraspecific variation in the stable isotope compositions. In stable natural habitats, different trophic niches are occupied by different collembolan species, but in disturbed habitats, poor niche specialization is partly compensated for by intraspecific trophic flexibility. The simplification of food-web structure was in line with the evidence coming from disturbed aquatic ecosystems, suggesting that the collapse of trophic-niche structure may be a common feature of disturbed communities across biomes.

**Key words:** belowground communities; Collembola; community disassembly; disturbance; isotopic niche; microarthropods; niche overlap; soil fauna; springtails; stable isotopes; trophic niche.

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## INTRODUCTION

The niche concept is an important element in ecological thinking and is traditionally considered the basis for species coexistence (Hutchinson 1959, Chase and Leibold 2003). The assembly of natural communities may be disaggregated into two niche-related processes; the first is environmental filtering, which assembles communities of similar species and thus results in niche overlap (Vellend 2010, Kraft et al. 2014), and the second is competition among species, leading to niche differentiation between those species (MacArthur and Levins 1967, Violle et al. 2011). The niche structure of a community is suggested

to evolve with the long coexistence of species, implying a relatively stable environment. Stable environments are characterized by predictable community composition with pronounced niche differentiation (Giller 1996). In contrast, environments that are highly variable and fragmented in space and time are predicted to have stochastic community composition and a widespread niche overlap between species (Giller 1996, Chesson 2000). This pattern received empirical support in, for example, grassland communities (Mason et al. 2011).

The trophic niche, a dimension of the ecological niche, characterizes the effect of species on other species within a community and thus, to a

large extent, is related to the ecosystem role of the species. Species with a broad trophic niche are successful in invading endemic communities or surviving disturbance (Bommarco et al. 2010, Dammhahn et al. 2017). Most empirical studies on the trophic-niche shifts in disturbed habitats have focused on the responses of individual species, while changes in trophic-niche structure at the community level have been studied only in aquatic systems (di Lascio et al. 2013, Hansen et al. 2018).

Community-wide metrics of trophic-niche structure may be retrieved using stable isotope analysis (Layman et al. 2007, Cucherousset and Villéger 2015). Stable isotope compositions of carbon and nitrogen in a consumer integrate information on the trophic level and basal resources of the consumer (Post 2002). Despite some recognized methodological limitations (Flaherty and Ben-David 2010, Boecklen et al. 2011), stable isotopes are efficiently mirroring trophic niches (Newsome et al. 2007, Rodríguez and Herrera 2013). Stable isotope analysis is an especially valuable tool for studying cryptic belowground communities with reticulated interactions (Digel et al. 2014, Potapov et al. 2018). For example, the method revealed pronounced niche differentiation in major groups of soil microarthropods that were previously considered as being nonspecialized omnivores (Schneider et al. 2004, Chahartaghi et al. 2005). Well-defined trophic-niche structure has been shown in various natural belowground communities (Pollierer et al. 2009, Potapov et al. 2016), but changes in niche differentiation with the transition to disturbed or unstable habitats were not addressed.

Here, we study the trophic-niche structure in several belowground communities in habitats ranging from natural and stable in time (forests and meadows) to disturbed and less stable in time (pastures and urban lawns). For the model object, we used Collembola (springtails), one of the most abundant and ubiquitous groups of soil fauna and one that can reach high densities in both natural and disturbed habitats (Kuznetsova 1994, 2009, Rusek 1998). By scaling the variability in stable isotope composition within species based on the total isotope variability within the community, we explored trophic-niche differentiation between collembolan species. We hypothesized that the ratio of interspecific to intraspecific

variation in trophic niches in collembolan communities would be higher in natural than in disturbed habitats.

## METHODS

Soil samples were collected in an array of locations in the western and southwestern parts of the Moscow region and within the Moscow city (Russia). In total, nine communities of four types were studied: three forests, two meadows, two pastures, and two urban lawns. Forests were represented by 100- to 130-yr-old spruce stands and treated as undisturbed ecosystems. Graminoid-forb meadows were treated as minimally disturbed ecosystems (one of the meadows was regularly mowed). Pastures were subjected to regular cattle grazing and thus were treated as intermediately disturbed ecosystems. Lawns were located within Moscow, were regularly mowed and occasionally subjected to various impacts typical for urban areas and thus represented highly disturbed ecosystems. Detailed descriptions of all studied communities are given in Appendix S1: Table S1. For the statistical analyses, sampled ecosystems were classified as natural without anthropogenic nutrient supply (forest and meadow) or disturbed with anthropogenic nutrient supply (pasture and urban lawn).

Field sampling was performed during 2009–2015. The long sampling period was unlikely to affect our conclusions since the variability of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Collembola was shown to be stable in time in natural conditions (Potapov et al. 2014) and during laboratory storage of soil and litter samples (Korotkevich et al. 2016). Each community was sampled once by randomly taking five samples of litter (if present) and the uppermost 5 cm of soil within an area of  $\sim 25 \times 25$  m. Each sample weighed 3–5 kg in order to obtain enough material for stable isotope analysis. Collembola were extracted with heat in modified Tullgren funnels with filament lamps and stored in 70% alcohol. Identification to the species level was performed under a LEICA microscope with 40–100 $\times$  magnification using appropriate identification keys (Fjellberg 1998, 2007). All species from a community that were abundant enough to allow triplicate analysis were subjected to stable isotope analysis. Those species represented approximately 80% of

the total biomass of Collembola in the studied communities. From one to 40 specimens of each species were pooled as one replicate to obtain enough biomass (100–400 µg dry weight); three to 12 replicates were analyzed for each species in each community (Appendix S1: Table S2).

Collembola were dried at 50°C for at least 48 h, weighed, and wrapped in tin foil. Stable isotope analysis was conducted using a Delta V Plus continuous-flow IRMS (Thermo Fisher Scientific, Bremen, Germany) coupled with an elemental analyzer located at the Joint Usage Center at the Institute of Ecology and Evolution, Moscow. The isotope compositions of N and C were expressed using conventional  $\delta$ -notation relative to the international standards (atmospheric N<sub>2</sub> and Vienna Pee Dee Belemnite, respectively). The mass spectrometer was calibrated against International Atomic Energy Agency reference materials (glutamic acid USGS 40 and USGS 41 and cellulose IAEA-CH<sub>3</sub>). The drift was corrected using internal laboratory standards (casein and acetanilide). The standard deviation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of the reference materials ( $n = 6\text{--}8$ ) was  $<0.15\text{‰}$ .

Statistical analysis was performed in R 3.4.0 (R Development Core Team 2007) with the R Studio interface 1.0.143 (RStudio, Boston, Massachusetts, USA). We were not able to scale the communities according to the isotopic variability in resources since it was not possible to measure  $\delta$  values in all types of detritus that serve as potential basal resources for the soil food web. As an alternative, we assumed that the variability in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Collembola reflected the variability in available resources (trophic niches) within each community. Thus, we scaled the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Collembola from 0 to 1, corresponding to the minimum and maximum  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values across the measured samples within each community (Cucherousset and Villéger 2015). Unscaled  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of Collembola and of baseline resources are given in Appendix S1: Table S2, Fig. S1. For scaled data, several community isotopic-niche metrics were calculated: (1) R statistic for multivariate analysis of similarities ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values) with species identity as the grouping variable (package *vegan*; Oksanen et al. 2011) as a proxy for trophic-niche differentiation between species. The resulting R statistic can vary between  $-1$  (intergroup variability  $\ll$  intragroup variability) and  $+1$  (intergroup variability  $\gg$  intragroup

variability). In our data, the R statistic varied between 0.14 (high niche overlap and low differentiation) and 0.9 (low niche overlap and high differentiation); (2) mean distance of species to the community centroid (CD) as a proxy for trophic diversity within a community (Layman et al. 2007); (3) mean nearest neighbor species distance (NND) as a proxy for trophic redundancy (Layman et al. 2007); and (4) standard deviation of nearest neighbor species distance (SDNND) as a proxy for evenness of the trophic-niche distribution (Layman et al. 2007). Layman metrics were calculated using the package *siar* (Jackson et al. 2011). The difference in the metrics between natural and disturbed habitats was tested with the Welch *t*-test in R. Data were displayed using *ggplot2* (Wickham 2009).

## RESULTS

Comparison of inter- and intraspecific variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values revealed strict niche differentiations in forests and meadows (the R statistic varied from 0.82 to 0.9) and low niche differentiations in pastures and urban lawns ( $0.14 \leq R \leq 0.37$ ), where isotopic niches of different species largely overlapped (Fig. 1). Among isotopic-niche metrics, the R statistic ( $P = 0.0011$ ) and CD ( $P = 0.0053$ ) were significantly higher in natural than in disturbed habitats, while NND and SDNND did not differ significantly (Fig. 2).

## DISCUSSION

Collembolan communities in pastures and lawns had significantly lower isotope niche differentiation than forests and meadows, which supports our main hypothesis. Developed trophic-niche structure in natural habitats may reflect competitive communities with competition preventing niches from overlapping (MacArthur and Levins 1967, Violle et al. 2011). Intraspecific competition was suggested to be the driver of collembolan community composition in a pine forest based on morphological and ecological trait dissimilarities among coexisting species (Widenfalk et al. 2016). Well-pronounced trophic-niche differentiation among species is typically found in temperate forest communities of Collembola (Chahartaghi et al. 2005, Potapov et al. 2016) and other

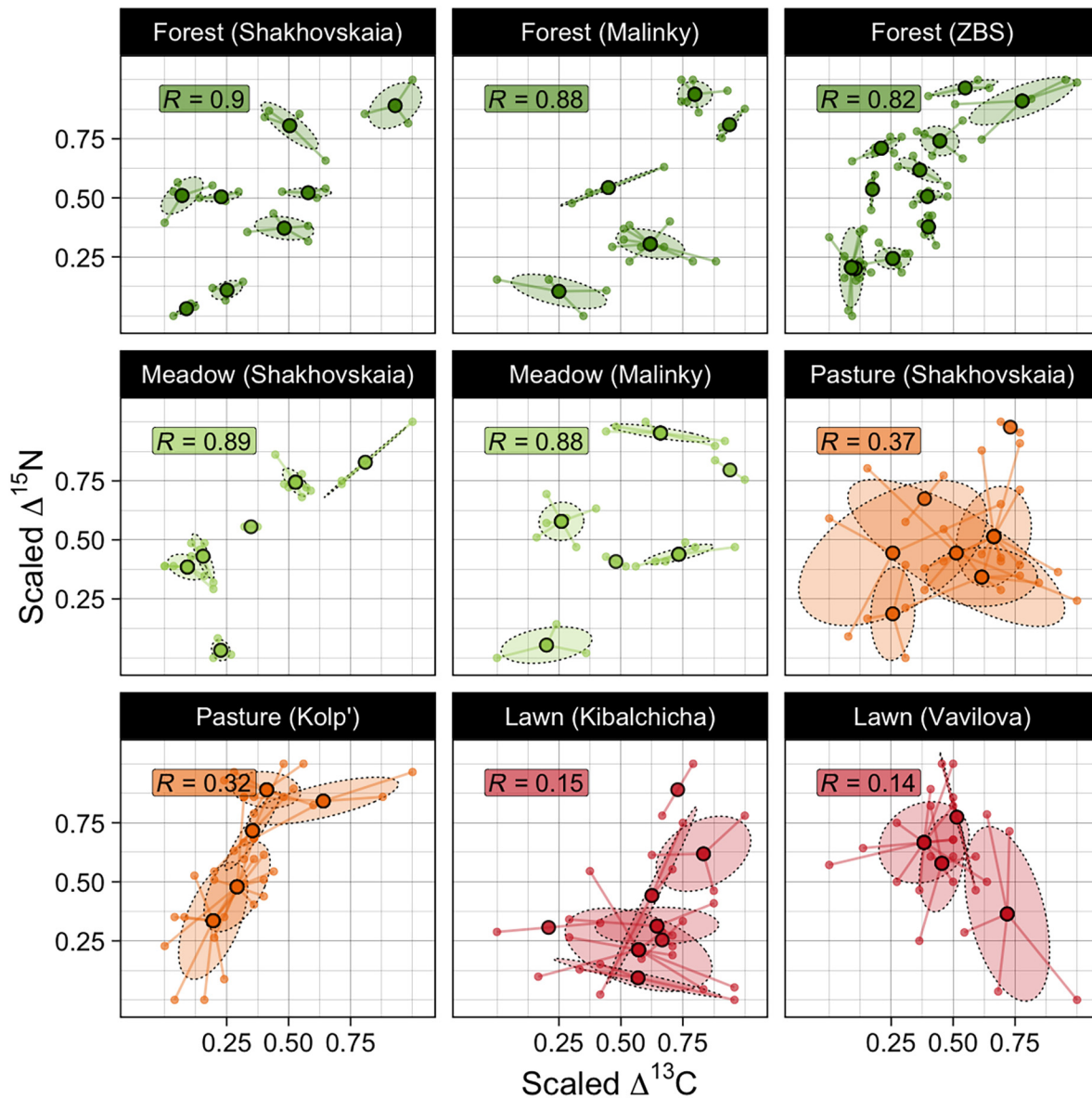


Fig. 1. Scaled stable isotope biplots of collembolan communities in different habitats. Small points represent individual samples and are connected to species' centroids (large circles); standard ellipses are shown for species with three or more replicates (siar package; Jackson et al. 2011). Colors denote different types of habitats: spruce forest (dark green), meadow (light green), pasture (orange), and urban lawn (red). In each community,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were scaled between 0 and 1 to account for potentially different isotope variability in basal food resources (Cucherousset and Villéger 2015). R statistics from the analysis of similarities of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values with species as the grouping variable are shown as the measure of trophic-niche differentiation (see *Methods*). For unscaled  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, please refer to Appendix S1: Table S2).

soil invertebrates (Schneider et al. 2004, Okuzaki et al. 2009, Pollierer et al. 2009). Trophic-niche differentiation was also shown for meadow/grassland communities of soil fauna (König et al. 2011,

Crotty et al. 2014). Since the trend observed in our study fits published results, the sampled communities in forests and meadows can be treated as a reliable control.



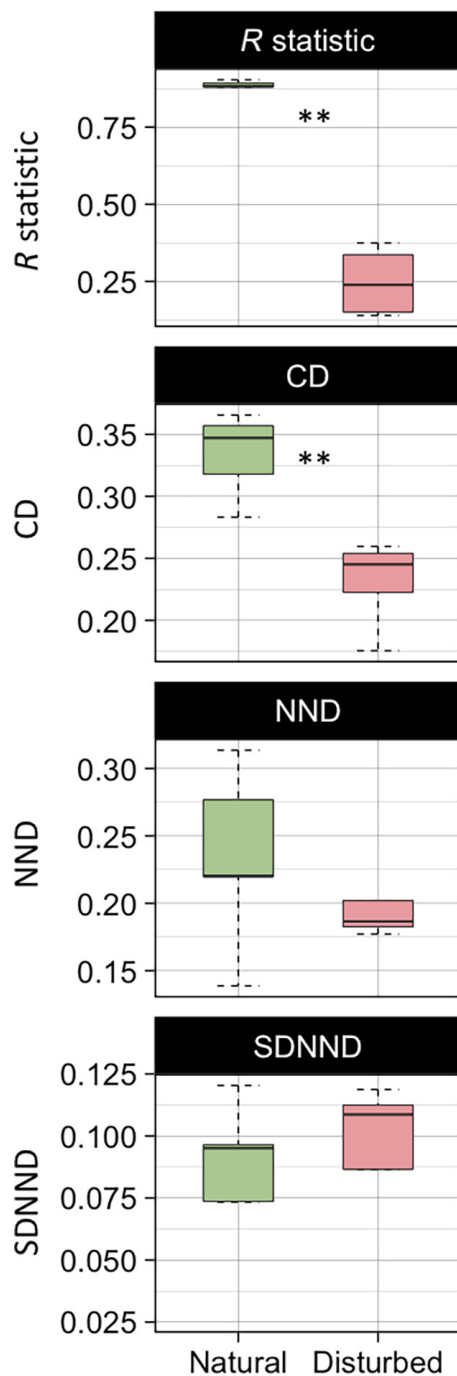


Fig. 2. Isotopic-niche metrics in collembolan communities from natural and disturbed habitats. Forests and meadows were grouped together as natural habitats ( $N = 5$ , denoted with green); pastures and urban lawns were grouped together as disturbed habitats ( $N = 4$ , denoted with red). The following metrics are shown: R statistic for the multivariate (scaled  $\delta^{13}\text{C}$  and

In pastures and lawns, the evident increase in the intraspecific isotope diversity relative to the total isotope diversity of the community suggests high trophic flexibility and a strong overlap of trophic niches among species. Noteworthy, isotopic distances between species (both NND and SDNND) showed similar pattern in natural and disturbed ecosystems thus hiding the underlying niche processes. This suggests a large loss of information caused by ignoring intraspecific variability while studying communities in disturbed habitats. The undeveloped trophic-niche structure is usually attributed to environmental- or biotic-filtering processes (Vellend 2010, Kraft et al. 2014), with communities being assembled of species with similar traits (Mayfield and Levine 2010, Widenfalk et al. 2015). In the case of disturbed habitats, such species are usually r-strategists and invasive species with a broad trophic niche (Gehring and Swihart 2003, Swihart et al. 2003, Bommarco et al. 2010). Invasive, compost, and ruderal collembolan species are often found in disturbed habitats, where they can reach high densities (Kuznetsova 1994, 2002, Leinaas et al. 2015). In the communities dominated by species with an opportunistic feeding strategy, an absence of external forces that restrict individual deviations in feeding habits from those of the rest of the population can be a sufficient condition for developing high between-individual diet variation (Svanbäck and Bolnick 2005, Araújo et al. 2011). In the absence of competitor species, interspecific competition decreases, while intraspecific competition increases, leading to higher individual specialization within a species (Van Valen 1965, Slatkin 1980, Araújo et al. 2011).

Reasons for limited competition in the disturbed habitats may include unstable and stochastic environments and/or a patchy resource supply. In particular, meadows and pastures differed greatly in trophic-niche structure. A well-developed trophic-niche structure in the meadow

(Fig. 2. Continued)

$\delta^{15}\text{N}$  values) analysis of similarities with species as the grouping variable; mean distance of species to community centroid (CD); mean distance to the nearest neighbor species (NND); and standard deviation of distance to the nearest neighbor species (SDNND). Differences between the natural and disturbed habitats were tested with the Welch  $t$ -test:  $^{**}P < 0.01$ .

communities was present despite occasional disturbance via mowing (Appendix S1: Table S1). Thus, the weak trophic-niche structure in the pasture communities is likely related to the presence of cattle. Cattle waste may form an important supply of labile nutrients below ground (Bardgett and Wardle 2003). Decomposing dung can be used by the majority of species in a community. Trophic link of different species to the same food resource was supported by a lower trophic diversity (CD) in communities of pastures, that is, all species were closer to the community centroid. As the supply of dung is random in space and time, the community composition of microsites in pastures is unpredictable and often dominated by a single species (Kuznetsova 2009). This situation of temporal dominance was described as the density compensation phenomenon (MacArthur et al. 1972, Chernov 2005), which creates conditions where interspecific competition decreases while intraspecific competition increases.

The studied city lawns are fragmented habitats that are subjected to occasional additions of soil organic matter and mowing. They are impacted by various pollutants and organic waste such as pets' excrements. The distribution of food resources and pollutants in urban environments is stochastic and highly heterogeneous (Pickett and Cadenasso 2009). The spatial and temporal variability creates a background for storage effects on population coexistence, where species survive in patchy populations and reproduce quickly under occasionally favorable conditions (Chesson 2000, Roxburgh et al. 2004). The situation resembles that in pastures and can explain the low trophic specialization.

Exploring the universality of the pattern reported in our study is challenging since to the best of our knowledge, no other studies have focused on the changes in trophic-niche structure under anthropogenic disturbance in below-ground communities. Evidence from ephemeral aquatic ecosystems suggests that food webs tend to increase in complexity and diversity with succession until the ecosystem collapses (Sargeant et al. 2010, O'Neill and Thorp 2014, Dalu et al. 2017a). Accordingly, stochastic environmental disturbances are likely to suppress development of stable trophic niches. A high similarity in trophic niches among species is also observed when resources are abundant but poorly

diversified (di Lascio et al. 2013) or scarce (Dalu et al. 2017b). Both eutrophication and resource limitation may increase with anthropogenic disturbance of natural habitats, leading to niche overlap. For instance, poor trophic diversity and low niche partitioning were observed in streams subjected to acidic pollution (Hogsden and Harding 2014) and to sediment disturbance in streams adjacent to agricultural landscapes (Burdon et al. 2018). These emerging similarities between our study and an array of studies in aquatic communities suggest that anthropogenic disturbances lead to similar responses in soil and aquatic ecosystems, creating communities with little niche differentiation. These communities are characterized by specific population dynamics and patterns of resource exploitation and are unlikely to be adequately described by the same models (or model parameters) as those developed for communities dwelling in more natural habitats. An emerging question is how the shift from communities where species occupy distinct trophic niches to communities where individuals within species occupy different trophic niches (thus playing the roles of species) will affect ecosystem functioning. Theory and experimental evidence suggest that niche specialization of species promotes ecosystem functions due to species complementarity (Loreau and Hector 2001). Thus, a negative effect of disturbance on ecosystem functions may be mechanistically explained by decreasing species specialization. This conclusion, however, remains to be tested in controlled experiments.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2528/full>