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Long-term effects on soil nematode community structure in spruce forests of removing or not removing fallen trees after a windstorm

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ABSTRACT

More than 12 000 ha of a Norway spruce forest in Tatra National Park, Slovakia, were laid down by a strong windstorm on 19 November 2004. Most of the broken and uprooted trees were completely removed from the area in the following months, but the remaining fallen trees were left in their natural successional state. We analysed the impact of these two strategies of forest management on the structure of the soil-nematode community and its relationships with the structure of the plant community and with basic soil physicochemical properties nine years after the windstorm. The relationships were investigated in a cleared windstorm plot (EXT), a non-extracted windstorm plot (NEX), and an undamaged forest plot (REF) as a control. All plots were sampled twice, in June and October 2013. Results showed that EXT and NEX had a significantly higher mean nematode abundance at both sampling dates than REF (LSD, $P = 0.05$). REF had the mean number of species, similar to the mean number in NEX. Analysis of variance showed significant main interaction among sampling time ($P = 0.01$), plots ($P = 0.05$) and number of species. Spearman's correlations identified positive correlations between the number of species and soil carbon and nitrogen contents ($P \leqslant 0.05$) and between the number of fungivores and soil nitrogen content ($P \leqslant 0.05$). A detrended correspondence analysis indicated that the abundance of plant parasitic nematodes was positively affected by the dominance of the grasses *Avenella flexuosa* in EXT and *Calamagrostis villosa* in NEX. Predators and root-fungal feeders were significantly less abundant in EXT and NEX ($P = 0.05$), and omnivores were most abundant in EXT and NEX. Analyses of the nematode communities by ecological and functional indices, except the plant-parasitic and enrichment indices, indicated that nematode abundance and species numbers did not differ between management strategies. The soil environments of all habitats could be characterised as mature, structured, nitrogen-rich, or nutrient-balanced with high or narrow carbon/nitrogen ratios, confirmed by an analysis of metabolic footprints. In summary, the impact of the windstorm on the soil-nematode community was still visible nine years later. The structure of the nematode community, however, had rehabilitated, likely due more to changes in the secondary herbaceous layer associated with the two management strategies than to the soil properties, which were not affected by the windstorm or management in the long term.

1. Introduction

Forests are species-rich terrestrial ecosystems supporting a wide range of taxa from numerous groups ranging from plants and vertebrates to canopy arthropods and soil microorganisms (Lindenmayer, 1999). This biological diversity is essential for the dynamics of forest ecosystems but is unfortunately exposed to harm. Windstorms are significant and key disturbances in most natural (unmanaged) forests (Ulanova, 2000) and affect not only trees and stands but can also change soil biota and initiate ground-layer successions (Peterson and Pickett, 1991). Ecologists have thus long studied the effects of windstorms of different extents, durations, intensities, or sizes on forest ecosystems, their dynamics, and rates of recovery to their original structure solely by natural succession (Ulanova, 2000).

More than 12 000 ha of a forest of Norway spruce (*Picea abies*) in Tatra National Park, Slovakia, were laid down by a strong windstorm on 19 November 2004. As much as 2 500 000 m^3 of timber were broken or uprooted. Most of the broken and uprooted trees were completely removed from the area in the following months, and the remaining fallen trees were left in their natural

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successional state. Several permanent research plots were established in the damaged area by the administration of the national park (Fleischer, 2008a) for the short- and long-term study of the impact of windstorm disturbance and management strategies on the restoration of the spruce-forest ecosystem. Another windstorm in May 2014, ten years after the first storm, unfortunately again damaged forests in the High Tatra Mountains, mainly at the site that had been monitored since 2004 as a control plot. The continued study of ecosystemic regeneration at the affected sites managed with different strategies was thus no longer possible.

Monitoring all taxa in a species-rich forest environment is not possible, so appropriate indicators must be chosen for monitoring ecosystemic changes (Lindenmayer, 1999). Indicators should (a) provide sufficiently early warnings of natural responses to environmental impacts, (b) have a broad geographical distribution or otherwise be widely applicable, (c) be relatively independent of sample size, and (d) be easy and cost effective to measure, collect, assay, and/or calculate (Noss, 1990). Various species of soil dwellers have been proposed and tested for their use as biological indicators of soil health and sustainability and for monitoring changes in the soil environment at spatial and temporal scales (Lindenmayer, 1999; Doran and Zeiss, 2000). Nematodes, collembolans, and mites are the most commonly used mesofaunal indicators (Tomar and Ahmad, 2009).

Nematodes are the most suitable indicators for environmental diagnoses based on the analysis of community structure, because their taxonomy and trophic roles are more precisely described (Gupta and Yeates, 1997) than for other groups of mesofauna. Nematodes exhibit many biological features (ubiquity, abundance, permeable cuticles, species richness, and easy sampling and assignment to trophic and ecological groups) that qualify them as good indicators of soil quality and soil disturbance, both at specific (taxonomic) and community levels (Bongers, 1990; Ferris et al., 2001). Nematode densities can reach several million individuals per square metre, and nematode communities of forests often comprise more than 100 species (Yeates et al., 2000). Species richness is generally higher in undisturbed than disturbed ecosystems (Neher et al., 2005). Soil moisture and relative humidity directly affect nematode survival because nematodes depend on water for locomotion and biological activity (Bongers, 1990; Ferris et al., 2001).

Other environmental and anthropogenic factors, however, can also distinctly influence the survival and composition of nematode communities and the presence of particular nematode species in natural forest ecosystems. Plants can affect soil organisms by several mechanisms – directly by generating above- and belowground inputs of organic matter and indirectly by physically shading and protecting soil and by taking up water and nutrients by their roots (Neher, 1999; Wardle, 2002). Energy and nutrients obtained by plants eventually become incorporated into detritus that provides the resource base for a complex soil food web. For example, plant roots exude amino acids and sugars that serve as a source of food for microorganisms (Curl and Truelove, 1986). Each plant root can be a source of food for plant parasitic nematodes. Dead roots are a source of food for bacteria and fungi (decomposition), which are a source of food for bacteriovorous and fungivorous nematodes, which are a source of food for predators.

Both management strategies (removal of fallen trees and natural succession) led to significant changes within the first four years after the windstorm in the plant communities of research plots established in the High Tatra Mountains (Šoltés et al., 2010), which affected microclimatic conditions, water and temperature regimes (Matejka and Fleischer, 2011), and the physical, chemical, and biological properties of the soils (Gömöryová et al., 2008; Šimonovičová et al., 2011). The removal of trees negatively affect the abundance and diversity of soil Collembola, Oribatida, and Nematoda during the first three years after disturbance (Čuchta et al., 2012; Lóšková et al., 2013; Čerevková et al., 2013). Svoboda et al. (2010), Šustek (2011) and Jonášová et al. (2010), however, reported that different strategies for the management of forests damaged by windstorms had a significant effect on ecosystemic regeneration. They suggested that not clearing windstorm damaged trees in protected areas was the best option for forest restoration and biodiversity.

On this basis, we hypothesised that changes in soil-nematode communities will not persist beyond the first few years after a windstorm and that different management strategies implemented in damaged areas could have considerable effects on the long-term rate of rehabilitation of nematode communities. The principal aim of our study was to compare the long-term impacts on nematode communities, such as changes in abundance, diversity, and community structure, associated with the plant communities and soil properties that arise from the implementation immediately after a windstorm of two management strategies: removing fallen trees or leaving them *in situ* for natural succession. We also identified the most sensitive taxa that could serve as indicators of forest-soil disturbance and secondary succession. This information will improve our understanding of the impact of forest management on communities of plant and soil nematodes and on recovery after disturbance and may be used as reference work for long-term bio-indication studies evaluating effect of various agents and activities disturbing forest ecosystems.

2. Materials and methods

2.1. Characteristics of the study plots

We studied the composition and structure of plant communities and the stage of regeneration after a 2004 windstorm in a spruce-forest soil ecosystem in two differently managed plots and undisturbed control plot by using soil-nematode communities as indicators. Each research plot had an area of 100 ha, and our study was realized on area of 100 m^2.

(1) Trees were removed after a windstorm in one plot (EXT; 49°07′N, 20°09′E) at 1040–1260 m a.s.l. and with a south-facing 10% slope. Before the windstorm, the site was covered by 90% *P. abies* and 10% *Larix decidua*. Šoltés et al. (2010) observed that the initial successional stage was composed of the understory of the original forest (e.g. *Vaccinium myrtillus*, *Oxalis acetosella*, *Hylocomium splendens*, and *Pleurozium schreberi*). The area was colonised by the heliophilous grass *C. villosa* in 2006, and *Chamaerion angustifolium* increased in abundance in 2007 and reached its maximum in 2011.
(2) The damaged forest was left unmanaged in another plot (NEX; 49°09′N, 20°15′E) at 1050–1150 m a.s.l. and with a south-southeast-facing 5–10% slope. Before the windstorm, the site was covered by 70% *P. abies*, 20% *Pinus sylvestris*, and 10% *L. decidua*. The fallen trees were in various stages of decay at the beginning of the study. The herbaceous layer within the first year after the windstorm was dominated by *C. villosa* and *Avenella flexuosa* (Šoltés et al., 2010). *C. angustifolium* became dominant in 2011 and *Rubus idaeus* in 2012 (Homolová et al., 2015).
(3) An intact reference forest stand (REF; 49°07′N, 20°47′E) at 1100–1250 m a.s.l. and with a southeast-facing 10–20% slope was not affected by the windstorm. Before the windstorm, the site was covered by a 120-year-old stand of 80% *P. abies* and 20% *L. decidua*. The ground vegetation, which did not change significantly during the study, was rich in mosses, spruce needles, *V. myrtillus*, and *O. acetosella* and