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Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of managed beech stands

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ABSTRACT

Understanding the processes driving biodiversity changes in forest communities helps to better evaluate sustainable forest management methods and their effects on forest ecosystems. This, in turn, is crucial for the appropriate management of protected areas, in particular those covered under the European protection program Natura 2000. Two datasets from the Polish Eastern Carpathians collected in the 1970s and 2000s were compared to analyse the temporal and spatial changes in the species composition of beech forests in a habitat gradient of soil moisture, acidity and fertility. We found that species favouring fertile and alkaline soils, with low ability for vegetative propagation and without a persistent seed bank became less frequent, whilst frequency of good competitors tolerant to lower soil pH and fertility with a persistent seed bank and a capacity for dispersing seeds over long distances increased. Herb layer vegetation on poor and rich soils became less similar in the past 30 years, though two opposite processes occurred. In poor habitats, the biotic differentiation of herb layer vegetation prevailed, whilst biotic homogenisation was more important in fertile habitats. It is suggested that the ageing of the managed beech stands might have contributed to these changes through the accumulation of litter, top soil acidification and the lowering of the concentration of nutrients as well as due to altered disturbance regimes in older stands. The observed relationships between biotic homogenisation/differentiation and the habitat gradient indicate that differences in soil conditions not only shape the spatial pattern of the forest vegetation, but also the spatial and temporal patterns of changes in vegetation composition resulting from the ageing of tree stands. Our results also suggest that in spite of continuous management the studied beech forests have only slightly changed in their specific species composition. Moreover, the ageing of tree stands did not necessarily generate better conditions for the conservation of the species richness of herbaceous plants, at least those species that are considered a measure of naturalness in beech forests.

1. Introduction

The long-term, variable use of forests by humans has resulted in an alteration of their habitats and species composition (Decocq et al., 2005; van Calster et al., 2007). Under anthropogenic influences, species that were unable to adapt to the altered conditions disappeared and were eventually replaced by those that coped well with the new conditions. The disappearance of the former and the spread of the latter have increased the similarity amongst forest patches and have simplified the structure of forest communities (McKinney and Lockwood, 1999; Rooney et al., 2004; Smart et al., 2006; Wiegmann and Waller, 2006). It appears that such changes in forest communities can be considered in terms of biotic homogenisation (BH) (Keith et al., 2009; Naaf and Wulf, 2010; Smart et al., 2006), which is defined as the increase in the similarity of biotas over time due to changes in species composition induced by the dispersal of some species and the disappearance of others (McKinney and Lockwood, 1999; Olden and Rooney, 2006). An increasing similarity between species assemblages is synonymous with a decrease in β diversity. Studies of the BH of forest communities are very often based on the comparison of the mean values of pairwise species-composition similarity indices between two or more temporal censuses. This method is largely equivalent to the variation conception of β diversity proposed by Anderson et al. (2011).

Ecological processes that change the species composition of vegetation are driven by migration, dispersal, abiotic factors and biotic interactions. In environments altered by humans, these processes sometimes function as filters which cause the disappearance of

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certain species and the dispersal of others (Matlack, 2005; Zobel et al., 1998). Many of the former species, called loser species, are stenotopic, whilst the latter ones, called winner species, are mostly eurytopic taxa (Naaf and Wulf, 2011). The potential mechanisms driving the process of forest homogenisation include forest management, eutrophication, increasing habitat shading and the excessive growth of large herbivorous populations (Keith et al., 2009; Naaf and Wulf, 2011; Rooney et al., 2004; Wiegmann and Waller, 2006). In this respect, it is important that forest management in Central Europe has changed considerably in the last several decades. Currently, forest tree stands have gotten older, more sustainable timber management has been applied and the exploitation of non-timber forest products has become less intensive than before (Kuemmerle et al., 2007). In particular, the ageing of European forests seems to be of great importance, making them less vulnerable to fire, but more susceptible to damage by wind and insects (Seidl et al., 2011). It can also be expected that older forests provide greater spatial diversity of resources and specific habitats, and thus contribute to the maintenance of a high biodiversity of species, especially those found only in old forests (Halpern and Spies, 1995; Humphrey, 2005; Peet and Christensen, 1988). In this way, old forests better fulfil requirements for the conservation of biodiversity of forest biocenoses, which is the main target of the Natura 2000 programme in European countries.

Most data on the BH of vegetation were obtained from large scale analyses (countries or continents) (Qian et al., 2008; Rejmánek, 2000; Smart et al., 2006), revealing the main directions and mechanisms of changes. However, reports on the taxonomic homogenisation of European vegetation are not consistent. On the one hand, Smart et al. (2006) found no evidence to suggest that there was taxonomic homogenisation at the level of the whole UK, whilst on the other hand, Keith et al. (2009) reported the taxonomic homogenisation of forests in southern UK, as did Naaf and Wulf (2010) in north-western Germany. Regardless of the final conclusions of those papers, it should be emphasised that they were based on pooled analyses of various plant communities, differing in management regimes and responses to disturbances. Therefore, it appears that due to the geographical variability of environmental conditions, different histories of forest vegetation and the wide range of natural and anthropogenic disturbances in large areas, only data collected at a smaller spatial (e.g. regional) scale can be applied in the diagnosis of the homogenisation of forest communities.

This paper presents an analysis of compositional changes in forest vegetation representing one regionally dominant forest type under various soil conditions that was arranged in a gradient of acidity and fertility. Temporal and spatial changes in species composition resulting from the ageing of tree stands and the variability of site conditions were studied in montane forests dominated by European beech (*Fagus sylvatica*), which is widespread in the mountains of Central Europe. The plant species composition of the herb layer was selected for analysis because of its variability and sensitivity to habitat conditions and various disturbances (Gilliam, 2007). In our study, we used old phytosociological data from the 1970s (Dzwonko, 1977) and compared them with data collected over thirty years later.

It has been shown that, along with the ageing of the beech stands, a thicker layer of beech litter has accumulated, which has resulted in top soil acidification and lower concentrations of nutrients as well as a shift from mull to moder humus observed along beech stand chronosequences (Barbier et al., 2008; Trap et al., 2011, 2013). Therefore, the change of soil conditions due to the ageing of the beech stands is more pronounced at less fertile sites than at more fertile ones because of the greater buffering capacity of the latter ones. Thus, we can assume that changes in species composition resulting from the stand's ageing in beech forests differ between less and more fertile habitats, and can in fact proceed in opposite directions. Since the role of interspecific competition that influence species richness is related to habitat fertility (productivity), we assume that in the studied forests the spread of more competitive winners is more pronounced at fertile sites (Grime, 1977; Pugnaire and Luque, 2001). We also predict that at more fertile sites the species with greater abilities to persist in the changing environment, i.e. generalists, are favoured and this results in the homogenisation of species composition amongst stands. Moreover, we expect that at less fertile sites less intensive competitive exclusion of specialists and their replacement by generalists takes place and the increase of compositional homogeneity is smaller.

Therefore, the objectives of this study are: (1) to find temporal changes in species richness and composition along a gradient of soil fertility in beech forests in the Carpathian Mountains over a thirty-year time window; (2) to detect if patterns of temporal changes in amongst-stand variability, i.e. homogenisation or differentiation, are related to habitat gradients; (3) to identify emergent groups of plants that are represented by loser and winner species and (4) to assess the conservation status of beech forests, taking into account species diagnostics for beech forests in the phytosociological system of plant communities that underlay the Habitat Directive for the Natura 2000 programme sites in the EU.

2. Material and methods

2.1. Study site

Data used in this study were collected in an area of the Sanocko-Turczańskie Mountains (northern part of the Polish Eastern Carpathians, part of the Natura 2000 site ("Słonne Mountains" PLH180013, PLB180003). The study area (about 46,000 ha, from 300 to 672 m a.s.l.) is composed of Carpathian flysch, upon which mostly acidic brown soils i.e. Eutric Cambisols have formed (Dzwonko, 1977; Skiba and Drewnik, 2003). The average annual temperature is 7.3 °C and annual rainfall is 814 mm (Michna and Paczos, 1972). The study area is characterised by high forest cover (about 65%) and the prevalence of beech forests with an admixture of fir and sycamore (about 30–40% of all forests) in the lower montane forest zone (Anonymous, 2007; Dzwonko, 1977). The majority of forests in this region are managed by the State Forest administration. Compared with the remaining part of Poland, this region has a larger percentage of old stands in the renewal class (i.e. mature stands subjected to simultaneous usage and renewal; renewal takes place under the cover of old trees and covers at least 30% of the stand) with variable tree age and height (ca. 25%, data for Brzozów, Brzegi Dolne and Lesko forest districts, Anonymous, 2007).

Forest management in this area was mainly based on the uniform shelterwood system. Since the socio-economic transformation in the 1990s, greater emphasis has been put on the sustainable management of forests in order to replace the dominant even-aged stands with uneven-aged ones, which are closer to nature – the uniform shelterwood system has gradually been replaced by the irregular shelterwood system. The most important changes in silvicultural methods concern: rotation age – 80–110 vs. 110–130 years; regeneration period – to 10 or from 10 to 20 vs. from 30 to 50 years (in the past and present respectively). At present, attention has also begun to be paid to keep old generation tree biogroups, old seed trees and deadwood during the renewal of stands. According to the management recommendation for the Natura 2000 programme (Herbich, 2004), a group selection system should be used with the natural regeneration of trees to achieve the species composition of tree stands in line with site conditions.