# TEMPORAL SPECIES TURNOVER AND PLANT COMMUNITY CHANGES ACROSS DIFFERENT HABITATS IN THE LAKE ENGURE NATURE PARK, LATVIA

Solvita Rūsiņa*[#], Ģertrūde Gavrilova**, Ieva Roze**, and Viesturs Šulcs**

\* Faculty of Geography and Earth Sciences, University of Latvia, Raiņa bulv. 19, Rīga, LV-1568, LATVIA;
rusina@lu.lv

\*\* Institute of Biology of the University of Latvia, Miera iela 3, Salaspils, LV-2169, LATVIA

[#] Corresponding author

*Simultaneous monitoring of vegetation dynamics in different ecosystems has been rarely conducted but can provide important insights into mechanisms of vegetation dynamics in relation to vegetation structure and patterns. We compared the herb layer dynamics, species turnover, and species-time relationships across different habitats in a 12-year period in the ILTER monitoring station of the Lake Engure Nature Park, Latvia. Temporal species turnover was defined as difference in species composition in a community between two times. Species-time relationships were assessed using a sliding window approach. Species richness, cumulative species richness, and diversity changed more in species-rich non-forest habitats than in forests. Species turnover was highly different among habitats, and was not associated with the stability of habitats, as reported from other studies. The species-time relationship of six habitats was much lower than that reported in the literature. This could be explained by latitudinal gradients in species diversity and temporal turnover. At higher latitudes both species diversity and turnover is lower, and the mentioned habitats represent typical boreal vegetation. Vegetation dynamics in acidic grassland, dune slack, fen, and dune forest were interpreted as fluctuations. Vegetation changes in moist forest, dry forest, and coastal grassland showed clear signs of succession (xerophytisation and overgrowing). Vegetation dynamics of the beach community exhibited features of both natural succession and anthropogenic fluctuation.*

**Key words:** *species-time relationship, succession, boreal forest, coastal vegetation, fen.*

## INTRODUCTION

The majority of permanent plot studies have been restricted to one vegetation type, and either to study natural succession or to evaluate the impact of particular disturbances (e.g. management type, fire event etc.) (Willems *et al.*, 1981; Bakker *et al.,* 1996; Block *et al.,* 2001; Smits *et al.,* 2002). Data on simultaneous monitoring of vegetation dynamics in several vegetation types is rare in the scientific literature (Smits *et al.,* 2002; Ozinga *et al.,* 2007; Kuiters, 2013). However, such data can provide important insights into the mechanisms of vegetation dynamics in relation to vegetation structure and patterns.

Fluctuation is a process of continuous changes in the community and appears as a mosaic pattern (e.g. temporal changes in dominant species) but not affecting the community as a whole (there is no development from one to another community). Succession is a process of vegetation development in the course of time leading to change from one

to another community. They are directional changes, and can be progressive or retrogressive succession leading to more or less complicated vegetation (van der Maarel, 1988; Laska, 2001). During succession new species enter a community and become dominant or diagnostic. In fluctuation dominant species do not change and new species entering community do not become diagnostic (Glenn-Lewin and van der Maarel, 1992). The border between fluctuation and succession is arbitrary. Although usually natural succession is observable in time periods not less than several decades (Glenn-Lewin and van der Maarel, 1992; Kollmann and Rasmussen, 2012) non-forest vegetation can experience rapid successional changes (Süss *et al.,* 2010; Ketner-Oostra *et al.,* 2012), and forest vegetation can regenerate from natural disturbances skipping one or more steps of succession (Heinrichs *et al.,* 2011).

Species turnover, species richness and vegetation structure (in terms of change in dominant species and species composition) are the most frequently used parameters to highlight

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the succession process (Glenn-Lewin and van der Maarel, 1992; Grime, 2002). The majority of papers dealing with species turnover focus on the spatial aspect (beta diversity) of the phenomenon (see a review in Rosenzweig, 1995; Gaston *et al.,* 2007). Temporal species turnover has been studied less but it is essential to understand the processes and patterns of species distribution and dynamics. Temporal species turnover can be reflected by species-time relationships. It is documented that more diverse ecosystems are more stable in time (Shurin, 2007). It depends on environmental variability and ecosystem type, and in this respect, the importance of long-term spatially comprehensive data from a broad range of ecosystems has been stressed in recent publications (Adler, 2004; White *et al.,* 2006; Magurran, 2007; 2010; Shurin, 2007; Magurran *et al.,* 2010).

The aim of the present research was to determine the patterns of vegetation development, species turnover and species-time relationship across different habitats.

## MATERIAL AND METHODS

**Study site.** In Latvia, simultaneous monitoring of several vegetation types has been carried out in the ILTER monitoring station of the Lake Engure Nature Park (Melecis, 2011). This area, nationally protected since 1957, is located in western Latvia and is a unique nature area at national scale from the viewpoint of biodiversity (Vīksne, 1997; Auniņš *et al.,* 2000; Gavrilova and Baroniņa, 2000; Laime, 2000) and physical geography (Eberhards and Saltupe, 2000). Lake Engure is located in the western part of the Coastal Lowland of Latvia and is separated from the Gulf of Riga by a 1.5- to 2-km wide dune strip. The climate is relatively mild and moist in the region. The average temperature is +5.7 $^{\circ}$C (the coldest month is February — minus 3.9 $^{\circ}$C, the warmest is July with +16.7 $^{\circ}$C). The last spring frosts are usually observed around May 23. The average annual precipitation is 590 mm. The vegetation period extends for about 180 days (Kļaviņš *et al.,* 2011).

The long history of protection has ensured the relatively undisturbed development of vegetation over the last 60 years both in forest and non-forest habitats. The Nature Park (terrestrial part covers 128 km$^2$) contains 856 vascular plant species, which is by 220 more species than would be expected from the average number per 128 km$^2$ according to the species-area relationship for Latvia (Laiviņš and Gavrilova, 2009). The area is little affected by plant invasions, most probably because large areas of natural and seminatural habitats remain (Gavrilova *et al.,* 2011). Among terrestrial ecosystems the largest areas are covered with dry to wet pine forests. Luxurious reed stands surround the lake, and calcareous fens and wet grasslands occur from place to place. Beach communities are common along the Riga Gulf shore. In 1842, the canal connecting the lake and the Riga Gulf was created. It led to overall lowering of the groundwater table near the lake and creation of wetlands along the shore (water receded for about 500 to 800 m). Until the first half of the 20th century, agricultural activities in the area

were mainly mowing and grazing in wet grasslands and even in the shallowest parts of the lake (Vīksne, 1997). Since the 1970s, the grasslands were mostly abandoned due to the nature protection paradigms at the time and a negative attitude of the Soviet government to private farming activities.

**Vegetation monitoring.** In total, 14 monitoring stations were established. The starting goal of the vegetation monitoring was to provide long-term vegetation data for entomological monitoring. Therefore, the selected location of each station was based on the needs of entomological monitoring. The aim was to cover the diversity of habitats of the Nature Park (Melecis *et al.,* 2000). Seven habitats were chosen in the spit of land dividing the lake from the Gulf of Riga, where the heterogeneous geomorphology (dune relief) and lowering of the water level in the Engure Lake created high vegetation diversity. Other stations were located on the other side of the lake in the drained lake bottom zone where a water body existed until 1840. For several reasons (e.g. problems in reallocation of plots or difficult access) only nine habitats were monitored each year and without interruption. Only data from those habitats were used in the present analysis (Fig. 1). 25% of the total indigenous vascular plant species of the Nature Park (Gavrilova and Baroniņa, 2000) were recorded in nine monitoring plots during the 12 year period.
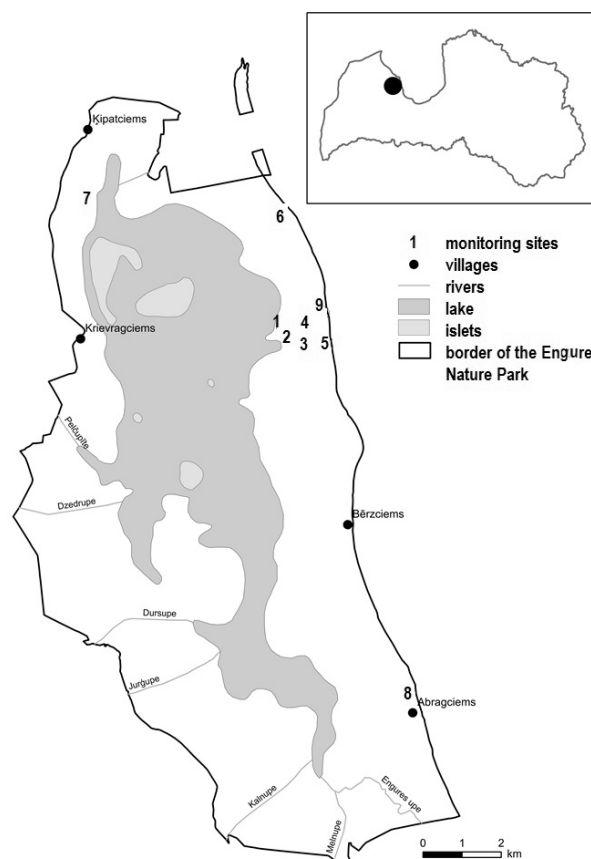


*Fig. 1.* Location of vegetation monitoring stations in the Lake Engure Nature Park. Stations used in the present study: 1 – acidic grassland, 2 – dune slack, 3 – moist forest, 4 – dune forest, 5 – beach, 6 – coastal grassland, 7 – fen, 8 – dry forest, 9 – mesic forest.

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Vegetation monitoring was carried out from 1997 to 2008 in the last week of June and first half of July by the same researchers in each of the sampling years. The size of a plot was 4 m$^2$ (2 × 2 m). Three pseudoreplicates were established in each monitoring station with a distance of 3 m between each plot. Plots were located in homogeneous parts of vegetation. All four corners were marked by wooden sticks to locate the plot each year. In addition, the closest large trees or other stable elements in the landscape were marked to relocate a plot if the sticks were lost (which was the case in several years in the beach habitat). Four sets of plots were established in forest vegetation (one moist and three dry-mesic pine forest sites, respectively), two plots were monitored in rich calcareous fens (one of them in a dune slack), one plot was established in a moist coastal grassland, one in a beach habitat with perennial herb vegetation, and one in acidic poor grassland (Table 1). Vascular plant species cover was estimated in percentages. Table 1

shows the assignment of monitoring site vegetation to the class and the alliance of phytosociological classification which was based on previous studies (Gavrilova *et al.*, 2011). Names of syntaxa follow the classification scheme of European vegetation by Rodwell *et al.* (2003). Assignment of monitoring sites to Natura 2000 habitat types defined in European Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora was done using the Interpretation Manual of European Union Habitats (Anonymous, 2007) and interpretation manual of EU habitats in Latvia (Auniņš, 2010).

**Data analysis.** The sampling design did not allow direct comparison among habitats as no replicates were available for each habitat type. Analysis was done based on combined plot data. In each monitoring site the average cover of each species was calculated from three pseudoreplicates (each in size of 4 m$^2$) for each year. This means that each combined

Table 1

DESCRIPTION OF MONITORING SITES

| Site No. | Name used in text | Geographical coordinates | Habitat and plant community | Dominant species in herb layer |
|---|---|---|---|---|
| 1. | Acidic grassland | N 57°17'17.7" E 23°08'30.3" | Fresh acidic grassland on poor soil (forest glade). *Koelerio-Corynephoretea, Plantagini-Festucion**; *Deschampsia flexuosa-Melampyrum pratense* com., do not correspond to any Natura 2000 habitat type. | *Deschampsia flexuosa, Melampyrum pratense, Anthoxanthum odoratum, Carex arenaria, Agrostis tenuis.* |
| 2. | Dune slack | N 57°17'13.9" E 23°08'57.8" | Wet calcareous dune slack *Scheuchzerio-Caricetea fuscae, Caricion davallianae; Schoenus ferrugineus-Phragmites australis* com. Natura 2000 habitat type 2190 Humid dune slacks. | *Schoenus ferrugineus* |
| 3. | Moist forest | N 57°17'1.8" E 23°09'01.9" | Moist pine forest in shallow dune slack *Vaccinio-Piceetea, Seslerio-Pineetum, Myrica gale-Pinus sylvestris* com. Natura 2000 habitat type 2190 Humid dune slacks. | *Myrica gale, Molinia caerulea, Equisetum variegatum, Vaccinium myrtillus* |
| 4. | Dune forest | N 57°17'20.4" E 23°09'13.2" | Dry pine forest on gray dune on acid soil *Vaccinio-Piceetea, Dicrano-Pinion; Carex arenaria-Pinus sylvestris* com. Natura 2000 habitat type 2180 Wooded dunes. | Herb cover sparse |
| 5. | Beach | N 57°17'19.3" E 23°09'51.3" | White dune on the beach overgrowing with perennial herbs *Ammophiletea, Ammophilion. Elymus arenarius-Festuca arenaria* com. Natura 2000 habitat type 2120 Shifting dunes along the shoreline with Ammophila arenaria (white dunes). | *Elymus arenarius, Elytrigia repens, Festuca arenaria.* |
| 6. | Coastal grassland | N 57°17'28.8" E 23°08'04.7" | Moist coastal grassland *Molinio-Arrhenatheretea, Calthion; Anthoxanthum odoratum-Carex nigra* com. Natura 2000 habitat type 1630* Boreal Baltic coastal meadows. | *Carex nigra, Anthoxanthum odoratum, Ranunculus acris, Hydrocotyle vulgaris, Trifolium pratense, Potentilla anserina.* |
| 7. | Fen | N 57°18'08.5" E 23°03'14.5" | Calcareous fen *Scheuchzerio-Caricetea fuscae, Caricion davallianae; Schoenus ferrugineus-Menyanthes trifoliata* com. Natura 2000 habitat type 7230 Alkaline fens. | *Myrica gale, Schoenus ferrugineus, Phragmites australis Menyanthes trifoliata* |
| 8. | Dry forest | N 57°10'41.4" E 23°13'16.5" | Dry pine forest on gray dune with neutral soil *Vaccinio-Piceetea, Dicrano-Pinion; Geranium sanguineum-Pinus sylvestris* com. Natura 2000 habitat type 2180 Wooded dunes. | *Geranium sanguineum, Festuca ovina, Vaccinium vitis-idaea, V. myrtillus, Orthilia secunda* |
| 9. | Mesic forest | N 57°17'23.0" E 23°09'41.3" | Mesic pine forest *Vaccinio-Piceetea, Dicrano-Pinion; Empetrum nigrum-Pinus sylvestris* com. Natura 2000 habitat type 2180 Wooded dunes. | *Vaccinium myrtillus, V. vitis-idaea, Empetrum nigrum.* |

plot represented an area of 12 m$^2$. Species diversity expressed as species richness and Shannon–Wiener diversity index (Kent and Coker, 1994). Sørensen similarity index was used to calculate similarity between the first year with each subsequent observation year.

Temporal species turnover was defined as a difference in species composition between two records in time. We measured species turnover for each possible pair of 12 years as a number of disappearances plus number of appearances divided by total number of species per both compared years (Milberg and Hansson, 1993; Pärtel and Zobel, 1995; Russell, 1998). The total species accumulation was determined as the difference between species richness in the first year of monitoring and cumulative species richness in the last year (van der Maarel and Sykes, 1993). Spearman rank correlation was used to correlate species diversity parameters and time (years). Analyses were conducted using SPSS 11.5.

Species-time relationships (STR) were constructed using a sliding window approach (White *et al.,* 2006; White and Gilchrist, 2007). Species richness was determined for every possible window of each time span: 12-year window, 11-year window, 10-year window etc. We averaged these values within each time span.

Then we used a power function to construct the species-time relationship in the form $S = cT^w$, where the constant c is the observed species richness at one year time-scale, and *w* is the slope of the STR.

The power function is recommended as more appropriate than the logarithmic function for comparing different ecosystems. This is because the power function suggests a constant percentage increase in species richness with each multiplicative increase in time scale, but the logarithmic function implies a constant absolute increase (see White *et al.,* 2006 for detailed comparison of power and logarithmic function for STR).

As no replicates were available for each habitat type, we could not use any tests to compare power function species-time relationships. Nevertheless, the comparative analysis of obtained species-time relationships provided insight into specific patterns of species turnover in time. Also, we were able to compare our results with other data, in the same way as e.g. White *et al.,* 2006 compared species-time relationships among different habitats without using tests.

An indirect ordination method Detrended Correspondence Analysis (McCune and Grace, 2002) was applied to study the variation in species composition among years. The software PcORD 5 was used (McCune and Mefford, 1999). The square-root transformation of species cover percentages and downweighting of rare species was applied. An after-the-fact coefficient of determination was calculated to characterize the quality of the data reduction, using the Euclidean distance in the ordination space and the Relative Euclidean distance in the original multidimensional space (McCune

and Grace, 2002). Environmental factors were passively plotted based on Ellenberg indicator values, and values were calculated (Ellenberg *et al.*, 1992).

Nomenclature followed Gavrilova and Šulcs (1999). We used taxa from the same genus not determined to species level in data analysis, but merged them into one taxon, e.g. all specimens of the genus *Agrostis* were not determined to species level, and thus species from different years were merged into one taxon of *Agrostis* species.

## RESULTS

**Vegetation dynamics.** Detrended Correspondence Analysis was used to reveal the main ecological gradients underlying the diversity of monitored habitats. Only the two first axes were interpreted as they accounted for the most of the variance. The after-the-fact evaluation of the DCA-ordination showed that 37% of the variance in the dataset was explained by axis 1, 18% by axis 2 and 10% by axis 3. Total inertia was 4.85, gradient length for axis 1 was 6.8 SD, Axis 2 — 5.2 SD, Axis 3 — 2.9 SD). The most important ecological gradient was moisture along the first axis and nutrients along the second axis. Relevés of each habitat consistently formed distinct clusters (Fig. 2).

As the habitats were strongly different, further analysis of vegetation dynamics was carried out separately for each habitat. Ordination of data from all years in DCA and passive correlation of Ellenberg indicator values and ordination axes were used to reveal if there were directional changes in vegetation (Tables 2 and 3; ordination diagrams not shown). Results of the DCA ordination indicated that the strongest changes in species composition occurred in the beach community. The gradient length of the first axis was 1.85, meaning that at least a half of changes in species composition had taken place during 12 years (Table 2). Other habitats had a gradient length from 0.75 to 1.28.
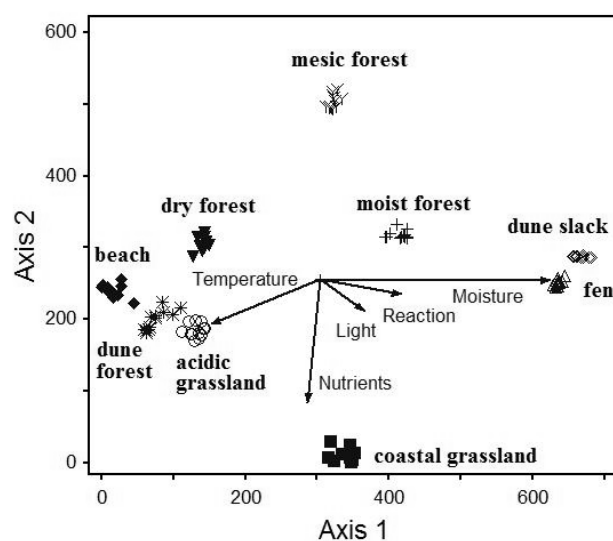


*Fig. 2.* DCA ordination of monitoring sites (based on vegetation data, all year observations were included).

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GRADIENT LENGTH AND IMPORTANCE OF FIRST TWO AXIS OF DCA ORDINATION OF ALL YEARS OF OBSERVATIONS PERFORMED SEPARATELY FOR EACH HABITAT

| Habitat | Gradient length for Axis 1 (SD)* | Gradient length for Axis 2 (SD) | After-the-fact $r^2$ for the Axis 1 and original multidimensional space** | After-the-fact $r^2$ for the Axis 2 and original multidimensional space |
|---|---|---|---|---|
| Acidic grassland | 0.97 | 0.73 | 0.28 | 0.17 |
| Dune slack | 1.28 | 0.88 | 0.59 | 0.02 |
| Moist forest | 0.98 | 0.88 | 0.78 | 0.05 |
| Dune forest | Lack of orthogonality | | | |
| Beach | 1.85 | 1.50 | 0.43 | 0.04 |
| Coastal grassland | 1.27 | 0.85 | 0.70 | 0.08 |
| Fen | 0.75 | 0.72 | 0.20 | 0.15 |
| Dry forest | 0.86 | 0.71 | 0.22 | 0.06 |
| Mesic forest | Lack of orthogonality | | | |

* gradient lengths expressed in standard deviation units;

** the importance of first two ordination axes evaluated by an after-the-fact coefficient of determination ($r^2$), using the Euclidean distance in the ordination space and the Relative Euclidean distance in the original multidimensional space

Acidic grassland experienced little changes in species composition. Cover of dominant species (*Deschampsia flexuosa* and *Melampyrum pratense*) fluctuated but no new species did override them in cover. Species composition indicated a change from dry and open grassland to denser and mesic grassland (Tables 3, 4) (*Silene nutans, Pilosella officinarum,* and *Veronica officinalis* disappeared; cover of *Poa pratensis, Galium album, Trientalis europaea, Veronica chamaedrys, Calamagrostis epigeios*, and *Lathyrus pratensis* increased significantly).

The dune slack habitat changed quite strongly, although dominant species (*Schoenus ferrugineus, Phragmites australis*) cover did not much change. No species decreased significantly but *Equisetum variegatum* and *Polygala amarella* disappeared. Several species appeared in the course of time or increased in cover – *Liparis loeselii, Eleocharis quinqueflora, Potentilla erecta, Cladium mariscus*, and *Molinia caerulea*. Moist pine forest dominated by *Molinia caerulea* and *Vaccinium myrtillus* in the ground layer changed in direction to a denser ground layer (high negative correlation of the first axis with the light Ellenberg values) and drier conditions ( decrease of several indicators of moist habitats like *Vaccinium uliginosum, Carex panicea, C. nigra, Myrica gale, Lycopus europaeus, Equisetum variegatum* and an increase in indicators of more mesic conditions, e.g. *Prunella vulgaris, Trifolium repens, Veronica officinalis*). On the other hand, some mesic species decreased as well (e.g. *Pyrola rotundifolia, Ranunculus acris,* and *Briza media*).

Dune forest with pines contained only six species in the ground layer (*Calamagrostis epigeios, Festuca ovina, Deschampsia flexuosa* (dominant), *Carex arenaria, Luzula pilosa,* and *Melampyrum pratense*) and the changes were negligible.

Beach vegetation was the most dynamic both in terms of species composition and dominant species. Three species dominated in all 12 years (*Festuca arenaria, Leymus arenarius* and *Carex arenaria*) and some species (*Galium album, Calamagrostis epigeios, Sedum acre, Linaria vulgaris, Elytrigia repens*) increased in cover for one-two years and afterwards decreased again or disappeared completely. Ellenberg indicator values indicated soil acidification during the study period.

ENVIRONMENTAL AND SPECIES DIVERSITY GRADIENTS OF THE DCA AXES 1 AND 2*

| Habitat | Year | Species number | Shannon index | Light | Temperature | Moisture | Reaction | Nitrogen |
|---|---|---|---|---|---|---|---|---|
| DCA Axis 1 | | | | | | | | |
| Acidic grassland | 0.85 | 0.13 | 0.12 | -0.59 | -0.34 | 0.57 | 0.28 | 0.66 |
| Dune slack | -0.73 | -0.34 | -0.29 | 0.32 | -0.48 | -0.08 | 0.09 | -0.05 |
| Moist forest | 0.94 | 0.38 | 0.12 | -0.63 | -0.21 | -0.58 | -0.26 | 0.11 |
| Beach | 0.42 | -0.22 | 0.05 | -0.03 | -0.28 | 0.15 | -0.64 | 0.20 |
| Coastal grassland | -0.88 | -0.25 | -0.49 | 0.62 | -0.21 | 0.53 | 0.55 | -0.40 |
| Fen | 0.73 | 0.11 | 0.64 | 0.26 | 0.21 | 0.05 | 0.21 | -0.11 |
| Dry forest | 0.85 | 0.05 | -0.14 | 0.17 | 0.30 | 0.08 | -0.26 | -0.11 |
| DCA Axis 2 | | | | | | | | |
| Acidic grassland | 0.06 | 0.46 | -0.30 | -0.25 | 0.38 | 0.53 | 0.09 | 0.38 |
| Dune slack | 0.15 | 0.21 | -0.05 | 0.20 | 0.22 | -0.32 | 0.06 | 0.17 |
| Moist forest | 0.09 | -0.10 | -0.31 | -0.05 | 0.55 | -0.15 | -0.14 | -0.02 |
| Beach | 0.15 | 0.21 | -0.05 | 0.20 | 0.22 | -0.32 | 0.06 | 0.17 |
| Coastal grassland | -0.09 | 0.22 | 0.12 | -0.19 | -0.21 | 0.02 | -0.24 | -0.03 |
| Fen | -0.12 | -0.14 | -0.21 | -0.26 | 0.02 | -0.35 | -0.15 | 0.50 |
| Dry forest | -0.12 | -0.11 | 0.17 | -0.17 | -0.03 | 0.08 | 0.29 | -0.20 |

* Axes, Spearman correlations with Ellenberg indicator values and species diversity indices. No correlations were available for dune forest and mesic forest as DCA failed with these data.

CHANGES IN ENVIRONMENTAL FACTORS AND SPECIES DIVERSITY DURING THE OBSERVATION PERIOD*

| Habitat | Species number | Shannon ndex | Light | Temperature | Moisture | Reaction | Nitrogen |
|---|---|---|---|---|---|---|---|
| Acidic grassland | -0.02 | 0.24 | **-0.82**\*\* | -0.45 | 0.57 | 0.45 | **0.76** |
| Dune slack | **0.60** | 0.35 | -0.43 | 0.51 | -0.29 | -0.07 | 0.11 |
| Moist forest | 0.47 | 0.26 | **-0.77** | -0.37 | **-0.71** | -0.29 | 0.17 |
| Dune forest | -0.36 | **-0.58** | -0.35 | **0.60** | **-0.61** | n | 0.36 |
| Beach | **-0.70** | -0.07 | 0.39 | -0.08 | -0.46 | **-0.63** | -0.17 |
| Coastal grassland | 0.41 | **0.67** | **-0.67** | 0.24 | **-0.74** | -0.57 | 0.51 |
| Fen | 0.12 | **0.73** | 0.49 | 0.45 | 0.06 | 0.39 | -0.25 |
| Dry forest | -0.13 | -0.40 | 0.13 | 0.57 | 0.06 | -0.43 | 0.01 |
| Mesic forest | -0.53 | **-0.61** | **-0.63** | **-0.82** | **0.78** | **-0.73** | -0.41 |

* Spearman rank correlations of year and Ellenberg indicator values and species diversity parameters. ** Correlation is significant at the 0.05 level

Coastal grassland changed in direction to dryer conditions and denser herb layer (Ellenberg values for moisture and light decreased (Table 3)). Species diversity increased in the course of time. A significant decrease in cover was observed for *Trifolium pratense, Galium palustre, Ranunculus acris*. Several low-growing species disappeared in four years (*Montia fontana, Juncus compressus, Carex panicea, Juncus gerardii*). Some species increased in cover for the first three-four years and afterwards decreased again (e.g. *Hydrocotyle vulgaris, Carex nigra, Achillea millefolium, Potentilla anserina*). The hygrophytes *Hydrocotyle vulgaris* and *Carex nigra* were dominants for the first nine years, but they were replaced by the hygromesophyte *Festuca arundinacea*, and the mesophyte *Agrostis tenuis* in the last three years.

Fen habitat experienced fluctuations in some species abundances from year to year (e.g. *Menyanthes trifoliata* fluctuated from 1% to 17% in cover) but there were no strong environmental gradients associated with the course of time (Table 3). There was a slight but significant decrease in cover of the dominant species *Schoenus ferrugineus*, as well as of *Phragmites australis*, *Drosera anglica*, and *Angelica sylvestris*. *Carex lasiocarpa* increased in cover during time. Several species disappeared (*Drosera rotundifolia, Dactylorhiza ochroleuca* and *D. incarnata, Carex nigra, Equisetum variegatum*), but only few species immigrated (*Carex pulicaris, Polygala amarella,* and *Salix starkeana*).

Dry forest experienced little change in species composition and cover. Only *Festuca ovina* decreased significantly in cover (from 12 to 1%). Other species were quite stable including the dominants *Vaccinium vitis-idaea, Fragaria vesca, Orthilia secunda, Geranium sanguineum*. Four species immigrated (*Pyrola minor, Stellaria graminea, Festuca arenaria,* and *Deschampsia flexuosa*), but six species disappeared (e.g. *Antennaria dioica, Solidago virgaurea, Poa pratensis, Campanula persicifolia*). Ellenberg indicator values showed that the most important environmental gradients in the ordination were moisture and soil reaction (Table 3).

The cumulative species richness of the mesic forest herb layer was only ten species. Nevertheless, some strong changes in species cover were observed. *Vaccinium myrtillus* increased twice (from 37 to 67 %) but *Empetrum nigrum* decreased from 35 to 5%. These changes as well as disappearance of *Pinus sylvestris* seedlings from the herb layer indicated decreased light conditions due to expansion of *Vaccinium*.

Correlations of Ellenberg indicator values and species diversity parameters with time (Table 4) indicated that all habitats with the exception of dry forest experienced environmental changes. Light availability decreased in four habitats, moisture decreased in three, and increased in one habitat, acidification was indicated in two habitats, and eutrophication of soil in one habitat. Species diversity parameters changed in all habitats but acidic grassland, moist forest, and dry forest (Table 4).

To describe the intensity of vegetation changes over 12 years, Sørensen dissimilarity index was calculated for 12 year observations and a mean index was obtained within each habitat. The most dynamic habitat was the beach, and the most stable habitat was the dune forest (Table 5). A

VEGETATION DYNAMICS OF NINE HABITATS MONITORED

| Habitat | Spearman rank correlation* | Mean Sørensen dissimilarity in 12 year period | Succession/ fluctuation |
|---|---|---|---|
| Acidic grassland | 0.009 | 0.20 | F |
| Dune slack | -0.018 | 0.21 | F |
| Moist forest | -0.700\*\* | 0.18 | S |
| Dune forest | -0.382 | 0.09 | F |
| Beach | -0.809\*\*\* | 0.33 | S |
| Coastal grassland | -0.882\*\*\* | 0.22 | S |
| Fen | -0.664\*\* | 0.17 | F |
| Dry forest | -0.773\*\*\* | 0.14 | S |
| Mesic forest | -0.909\*\*\* | 0.13 | S |

* Spearman rank correlation was calculated for year and Sørensen similarity index between pairs of the first year and each subsequent year.

** Correlation is significant at the 0.05 level

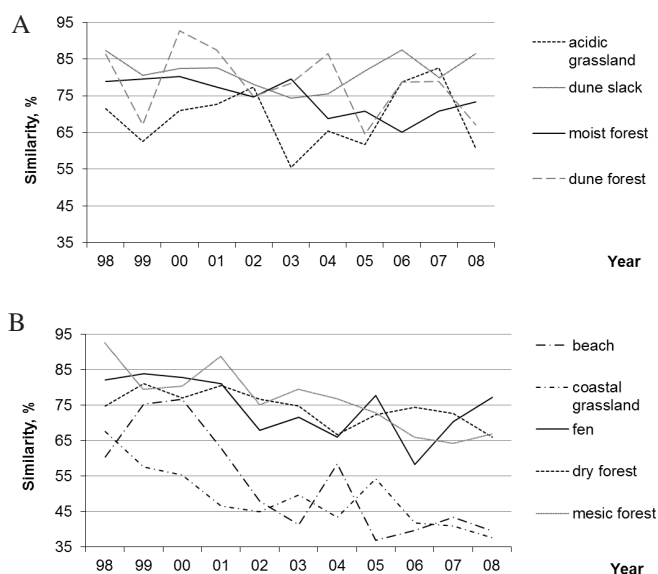*** Correlation is significant at the 0.01 level

*Fig. 3.* Change in percentage similarity in floristic composition (Sørensen similarity index) between the first observation year (1997) and each subsequent year. A – habitats with expressed fluctuation in similarity of floristic composition; B – habitats with a tendency to decrease in floristic similarity.

comparison between the first observation year and each subsequent year showed that some habitats changed substantially (Fig. 3).

**Species diversity, turnover and species-time relationship.** Species richness in the herb layer differed considerably among habitat types, ranging from 3 (dune forest) to 26 (coastal grassland) species per 4 $m^2$ plot in 1997. Combined plots (3 replicates of 2 × 2 m) contained more species ranging from 6 (dune forest) to 40 (coastal grassland). Species richness decreased significantly only on beach, but a significant decrease in species diversity (Shannon-Wiener index) was observed in dune forest and mesic forest. Species richness increased continuously in dune slack, fen, and coastal grassland. Other habitats experienced fluctuations in species richness and Shannon–Wiener diversity index (Table 6).

Cumulative species richness did not differ from the actual species richness in mesic forest and dune forest because only one new species appeared in these habitats during 12 years (*Listera cordata* and *Pinus sylvestris*, respectively). Other habitats experienced considerable divergence between number of species in the first year and cumulative species richness (total number of species in monitoring period), indicating that species immigration was intensive over 12 years (Table 7). The accumulation of species ranged from 1 species in dune forest and mesic forest to 36 species in coastal grassland. When expressed in percentages, cumulative species richness increased from 11% in dune forest to 147% in beach. Moreover, species appearance was not accompanied by species loss in fen and moist forest in the first three-four years, resulting in diversification of the herb layer of these habitats.

The highest species turnover was observed in the beach community, where it reached up to 70% (if compared the first with the last year). Rather high species turnover (up to 50–60%) was observed also in moist and mesic forest, and in both grassland habitats. Less dynamic species composition was found in dune slack, fen, dune forest and dry forest — turnover reached only 40–50%. Acidic grassland, dune slack and coastal grassland showed a similar course of species turnover. The same was true for acidic grassland and moist forest. Moist forest was similar also to fen, and dune forest and mesic forest did not differ. The amplitude of turnover was low in moist forest and both grassland habitats. A higher amplitude of change was observed in dune slack, fen and dry forest where species turnover changed between 20 and 30%, but in beach and mesic forest, turnover in the same time period for individual pairs differed between 0% and 50% or even 68% (on beach) (Fig. 4).

Species-time relationships were quite different between habitats (Fig. 5). The power function exponent ranged from 0.07 to 0.41. The steepest slope ($z = 0.41$) was observed on beach, followed by coastal grassland and dune slack (0.23 and 0.22, respectively). A low slope was shown in mesic and dune forest (0.07 and 0.08); other habitats were characterised by exponents from 0.11 to 0.16.

Table 6

SPECIES DIVERSITY CHANGES BETWEEN THE FIRST AND THE LAST YEAR AND DURING THE OBSERVATION PERIOD

| Habitat name | Mean number of species per 4 $m^2$ plot 1997/2008 | Shannon-Wiener index per 4 $m^2$ plot 1997/2008 | Number of species per combined plot 1997/2008 | Shannon-Wiener index per combined plot 1997/2008 | Correlation of species number per combined plot and year | Correlation of Shannon-Wiener index per combined plot and year |
|---|---|---|---|---|---|---|
| Acidic grassland | 11.3/13.0 | 1.21/1.46 | 22/21 | 1.40/1.70 | -0.02 | 0.24 |
| Dune slack | 6.7/8.3 | 0.88/0.90 | 11/15 | 0.92/0.93 | 0.60* | 0.35 |
| Moist forest | 17.0/22.7 | 1.79/2.13 | 33/39 | 2.36/2.61 | 0.47 | 0.26 |
| Dune forest | 3.3/3.3 | 0.71/0.67 | 6/5 | 0.94/0.53 | -0.36 | -0.58* |
| Beach | 13.0/10.0 | 1.89/1.85 | 21/16 | 2.15/1.91 | -0.70* | -0.07 |
| Coastal grassland | 26.3/27.7 | 2.36/2.44 | 40/44 | 2.74/3.00 | 0.41 | 0.67* |
| Fen | 16.7/22.7 | 1.13/1.67 | 30/35 | 1.48/2.07 | 0.12 | 0.73** |
| Dry forest | 20.0/22.3 | 2.38/2.19 | 39/38 | 2.94/2.73 | -0.13 | -0.40 |
| Mesic forest | 5.7/4.7 | 0.97/0.69 | 9/7 | 1.14/0.87 | -0.53 | -0.61* |

* Spearman rank correlation is significant at the 0.05 level

** Spearman rank correlation orrelation is significant at the 0.01 level

Table 7

SPECIES RICHNESS AND CUMULATIVE SPECIES RICHNESS IN MONITORED HABITATS

| Year/Habitat | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | Accumulation** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Acidic grassland | 22* | 21 | 19 | 19 | 17 | 22 | 19 | 20 | 18 | 19 | 22 | 21 | 8/36% |
| | 22 | 23 | 24 | 25 | 25 | 26 | 26 | 27 | 27 | 29 | 30 | 30 | |
| Dune slack | 11 | 11 | 12 | 13 | 10 | 15 | 15 | 12 | 11 | 15 | 15 | 15 | 11/100% |
| | 11 | 13 | 14 | 15 | 15 | 17 | 19 | 19 | 19 | 21 | 22 | 22 | |
| Moist forest | 33 | 33 | 38 | 38 | 34 | 33 | 36 | 35 | 34 | 37 | 37 | 39 | 19/57% |
| | 33 | 36 | 41 | 41 | 41 | 43 | 46 | 46 | 46 | 48 | 51 | 52 | |
| Dune forest | 6 | 6 | 6 | 6 | 5 | 6 | 7 | 5 | 4 | 7 | 5 | 5 | 1/16% |
| | 6 | 6 | 6 | 6 | 6 | 6 | 7 | 7 | 7 | 7 | 7 | 7 | |
| Beach | 21 | 24 | 21 | 19 | 21 | 30 | 16 | 18 | 18 | 17 | 19 | 16 | 31/147% |
| | 21 | 26 | 28 | 29 | 31 | 44 | 46 | 48 | 48 | 49 | 52 | 52 | |
| Coastal grassland | 40 | 37 | 46 | 44 | 38 | 45 | 40 | 40 | 47 | 54 | 43 | 44 | 36/90% |
| | 40 | 46 | 54 | 55 | 57 | 63 | 66 | 68 | 69 | 74 | 75 | 76 | |
| Fen | 30 | 29 | 36 | 38 | 36 | 39 | 35 | 38 | 38 | 33 | 34 | 35 | 18/60% |
| | 30 | 34 | 39 | 40 | 41 | 44 | 45 | 46 | 46 | 46 | 47 | 48 | |
| Dry forest | 39 | 40 | 39 | 36 | 36 | 37 | 34 | 36 | 37 | 40 | 38 | 38 | 12/30% |
| | 39 | 44 | 45 | 45 | 45 | 46 | 46 | 48 | 49 | 51 | 51 | 51 | |
| Mesic forest | 9 | 8 | 8 | 8 | 9 | 9 | 7 | 6 | 6 | 8 | 8 | 7 | 1/11% |
| | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 10 | 10 | 10 | 10 | |

* the first row is species richness and the second row is cumulative species richness

** accumulation is expressed as difference in cumulative species number of the last year and species number of the first year where the first figure is species number and the second — accumulation of species in per cent
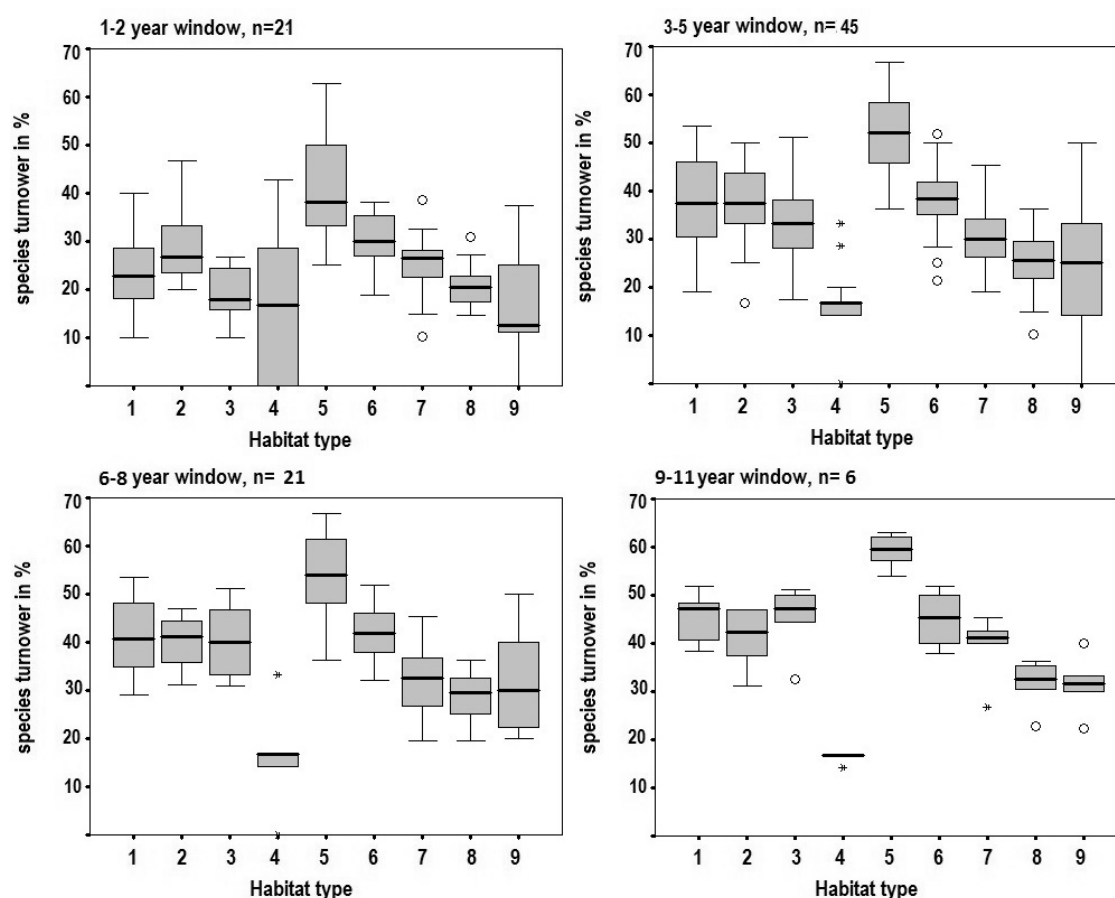


*Fig. 4.* Boxplots of amplitude in species turnover in the course of time for nine habitats monitored. Habitat type: 1 – acidic grassland, 2 – dune slack, 3 – moist forest, 4 – dune forest, 5 – beach, 6 – coastal grassland, 7 – fen, 8 – dry forest, 9 – mesic forest.
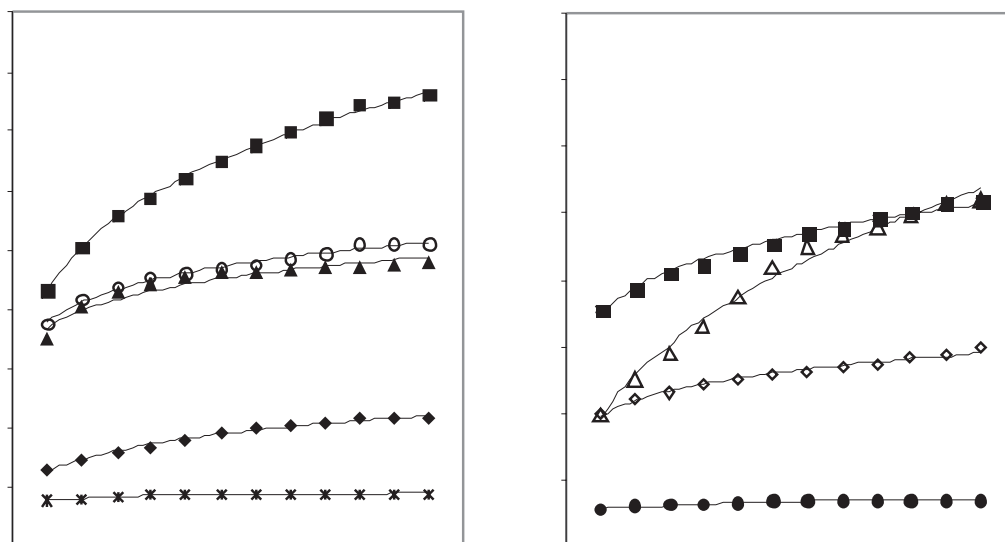
*Fig. 5.* Power function of species-time relationship in nine habitats monitored.

## DISCUSSION

**Species diversity, temporal turnover and species-time relationship.** Species richness did not change significantly in most habitats. This was an expected result for the 12 year period bearing in mind that no observable disturbances occurred in these habitats. Increase in species number in the dune slack (from 11 to 15 species per combined plot) can be explained by natural succession from sparse vegetation to more closed vegetation as organic matter and nutrients accumulate and the edaphic environment becomes less extreme. The age of the dune slack was about 130–160 years (Eberhards and Saltupe, 2000). Such a succession is in accordance with other investigations (Grootjans *et al.,* 1991; Sżkora *et al.,* 2004). Species richness decreased in the beach community (from 21–24 to 16–18 species per combined plot) in response to anthropogenic disturbances, such as travelling by cars through the area, and natural processes (herb layer damage in storms). Species composition also indicated acidification of soil, a process documented in other dune systems (Sival *et al.,* 1997; Ketner-Oostra and Sykora, 2000; Sykora *et al.,* 2004).

The Shannon–Wiener diversity index increased significantly in coastal grassland and fen, and decreased in dune and mesic forest. Neither increase nor decrease of the diversity index was accompanied by significant changes in species richness (although tendencies were the same). This means that the main changing component of diversity was evenness. It was expected that diversity will decrease in coastal grassland and fen as the traditional management has been ceased for several years. The normal course of succession in such conditions is overgrowing by shrubs with simultaneous decrease in vegetation diversity (Ellenberg, 1996). Ellenberg indicator values showed xerophytisation of soil in both habitats, and encroachment of *Cladium mariscus* in fen, and mesophytic species like *Agrostis tenuis* and *Festuca pratensis* were outcompeting hygrophytic ones (e.g. *Hydrocotyle vulgaris, Carex nigra*) in grassland. The

diversification of the herb layer is probably temporary in these habitats and species diversity may decline again in the course of succession. Decrease of species diversity in dune and mesic forest cannot be explained ecologically as too few species formed the herb layer (in total only seven species). Fluctuations of species diversity (not directional changes) in dry and mesic pine forests have been observed within the same period of time in western and central Latvia (Laiviņš *et al.,* 2007).

Species turnover is continuous, even in communities that are not undergoing directional change. The total number of species recorded at a given locality will rise with time (Preston, 1960; Magurran, 2007). Cumulative species richness was quite similar to findings in other studies, and ranged from 16% to 147% in different habitats. Van den Maarel and Sykes (1993) reported that species number increased by about 30% in 2 m$^2$ in a six-year period in dry grassland. Chytrż *et al.* (2001) observed cumulative species richness in dry heathlands to increased by 170% from the initial number of species in highly disturbed heathland and by 60% in undisturbed heathland in an eight-year period. White *et al.* (2006) observed that species numbers almost doubled during ten years compared with the single-year species richness (similar tendency in different habitats and taxonomic groups). Cumulative species richness was higher in shallow soil (100%) than on deep soil (88%) in a dry grassland in Poland during a four-year period (Baba, 2004).

Our results showed the same tendency as observed in the above mentioned studies — cumulative species richness was higher in dynamic habitats than in stable habitats. Beach (the most disturbed habitat) had the highest cumulative species richness followed by dune slack and coastal grassland, which experienced rapid changes in habitat conditions — overgrowing in grassland and overgrowing plus changes in moisture regime in the slack. Among other habitats, moist habitats had higher cumulative species richness (accumulation was above 50%) than dry and mesic habitats

(accumulation was below 40%). Nevertheless, it cannot be concluded that moist habitats are more dynamic as vegetation composition showed changes in moisture regime (Ellenberg value for moisture decreased) in both mesic and moist habitats over 12 years, indicating successional changes in the moisture regime at the Nature Park scale. The data for the Lake Engure drainage basin show that for the last ~80 years the increase of annual mean temperatures indicated warming, and the water level in Lake Engure was decreasing in the period from 1998 to 2006 (for about 40 cm) (Kļaviņš *et al.,* 2011).

Greater accumulation of species in moist habitats indicated that their vegetation reacted to changes in moisture regime much faster than in dry and mesic habitats. Temporal species turnover and species-time relationship results from local colonisation and extinction of species governed by fluctuations in environmental factors, dispersal limitation or succession (White and Gilchrist, 2007).

High species turnover is observed mainly in dynamic situations — semi-natural vegetation or vegetation experiencing regular disturbances, e.g., dune and beach vegetation (Milberg and Hansson, 1993; van der Maarel and Sykes, 1993; White *et al.,* 2006). Climatic or edaphic climax vegetation normally has lower species turnover (but can be rather high at small scale (Pärtel and Zobel, 1995)), which increases dramatically after severe disturbance, e.g. in burned heathlands (Chytrż *et al.,* 2001). Ecosystems dominated by annual growth forms and more plants with ruderal strategy show higher species turnover than those with perennial dominants and more stress-tolerators (Chytrż *et al.,* 2001, Krieger *et al.,* 2003). On the other hand geophytes and hemicryptophytes can persist in a plot only in root form (thus not encountered as existent in species counts in certain years) or can be short-lived and thus mobile (van der Maarel and Sykes, 1993). Grassland vegetation can be with low turnover if species dominating the vegetation are slow-growing and stable, like tussock-forming *Festuca* species in steppic grasslands (Baba, 2004).

We found that high species turnover was associated not only with dynamic habitats but also with comparatively stable ones — moist forest, dune slack, and mesic forest. High turnover of moist forest and dune slack can be explained by changes in the environment which have led to successional changes in vegetation. Due to low total species diversity, the pattern observed in mesic forest may, however, be more influenced by stochastic factors than in moist forest and dune slack.

In general, species turnover amplitude (range of turnover index values in the same habitat over the same time span) decreased in all habitats with increasing time span, irrespective of habitat type. It was more than 20% in some habitats for the 1–2 year period, but less than 10% in all habitats for the 9–11 year period. This means that only with sufficiently long temporal gradient the character of temporal turnover of an ecosystem will appear. For example, the beach community experienced a turnover from 25% to 68% in 1- to 2-

year period. Thus, the species mobility can be both very high and rather low in this habitat in the same time span, and we cannot predict the amplitude of change of this habitat for short periods. However, for longer time periods (in our case 9–11 years), the beach is a highly unstable habitat, as species composition changed by about 60% in a 10-year period. There are almost no data in the literature about the amplitude of turnover across different time spans, and therefore it was not possible to compare if this finding reflects the common pattern or is an exception. The data provided by Russell (1998) indicates that in bird communities this pattern can be inverted, or possibly the pattern depends on a time span. The range of turnover index was narrower in short time periods (1–5 years) and broader in longer time periods (up to 80 years).

There is a negative relationship between species richness and temporal turnover, i.e. the species-time relationship (STR) is less steep in more diverse habitats (White *et al.,* 2006; Shurin, 2007). Our data supports this finding only partly. The highest value of the STR exponent (0.41) was in the environmentally most variable habitat — beach, which had intermediate species richness, but the second highest STR exponent was in coastal grassland — the most species rich habitat. The most species poor habitats (mesic forest and dune forest) had the lowest STR exponent (0.07 and 0.08).

**Vegetation dynamics.** The studied dabitats could be divided into two categories according to the patterns in vegetation dynamics — fluctuation and succession. Vegetation changes were assessed as fluctuations when changes were chaotic, similarity among first and subsequent years was not decreasing constantly, time was not an important gradient in DCA ordination and year did not correlate with any environmental factor, and also species turnover did not increase over larger time periods when compared with shorter ones. We classified vegetation dynamics as a succession when changes led to ever lesser similarity between years (Table 5) combined with high correlation of time (years) with Ellenberg values or species diversity parameters and increasing species turnover over time. Of course, if the monitoring was continued, successional changes can appear as a fluctuation if longer time periods are considered.

Vegetation dynamics in acidic grassland, dune slack, fen, and dune forest were interpreted as fluctuations. Species turnover in acidic grassland was increasing within longer time spans and vegetation changes indicated shifts in environment (increasing moisture and decreasing light). On the other hand, similarity between the first and subsequent years did not decrease continuously (2007 was the most similar to 1997). It seems that for about eight years vegetation changed directionally, but further on some environmental fluctuations reverted herb layer vegetation back to preceding conditions.

Regarding dune slack and fen, although species accumulation was high (100%), other parameters did not show clear successional changes. A large local species pool could be responsible for high species accumulation (van der Maarel

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and Sykes, 1993; Krieger *et al.,* 2003). The situation was similar in calcareous fen vegetation, which is very common in the Engure Nature Park, which contains a species rich flora (Auniņš *et al.,* 2000; Gavrilova and Baroniņa, 2000).

The species poor dune forest was stable with only small fluctuations in the herb layer.

Vegetation changes in moist forest, dry forest, and coastal grassland showed clear signs of succession. All parameters of moist forest showed directional changes. Similarity decreased significantly and continuously, the first axis of DCA ordination was closely correlated with time, and the species composition indicated decreases in moisture and light. Species turnover increased steadily and species accumulation was rather high. This could be induced by warming during the last 80 years and a decrease of water level starting from 1997 (Kļaviņš *et al.,* 2011).

It is not clear what will be the final stage of dry forest succession if the observed changes will continue. Although species composition changed continuously (similarity decreased steadily and DCA ordination showed correlation between time and species composition) no indication of shift in environment could be detected by Ellenberg indicator values. Species accumulation was low and turnover did not rise with increasing time. It is supposed that the observed changes disclosed intrinsic alteration of the herb layer community taking place during the ageing of the forest stand.

Coastal grassland is overgrowing and will turn into forest if not disturbed. Temporal species turnover and other parameters indicated that the grassland experienced a short flourishing period (increase in species diversity after reduced pressure of disturbances) after abandonment of mowing.

Vegetation dynamics of the beach community exhibited features of both succession and fluctuation. Most parameters were the highest in this habitat. Decreasing of similarity in species composition was very pronounced, DCA ordination revealed that the main explanatory variable of the change in species composition was time, Ellenberg indicator values indicated soil acidification, species accumulation was the highest, and species-time relationship was the steepest. Nevertheless, it was obvious that natural succession (vegetation development from sparse vegetation of white dunes to denser vegetation resembling grey dunes) was overlaid by anthropogenically induced fluctuations. Both processes created a pattern showing that along with decreasing similarity of vegetation, temporal turnover was variable.

REFERENCES

Adler, P. B. (2004). Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. *Ecology*, **85** (5), 1265–1272.

Adler, P. B., Lauenroth, W. K. (2003). The power of time: Spatiotemporal scaling of species diversity. *Ecol. Lett.,* **6**, 749–756.

Anonymous (2007). *Interpretation Manual of European Union Habitats.* EUR 27. European Commission DG Environment.

Auniņš, A. (Ed.) (2010). *Eiropas Savienības aizsargājamie biotopi Latvijā. Noteikšanas rokasgrāmata* [European Union Protected Habitats in Latvia. Manual]. Rīga: Latvijas Dabas fonds. 320 lpp. (in Latvian).

Auniņš, A., Zviedre, E., Brūmelis, G. (2000). Preliminary results of remote sensing based vegetation mapping of Lake Engures (Engure), Latvia. *Proc. Latvian Acad. Sci. Sect. B*, **54** (5/6), 170–176.

Baba, W. (2004). The structure and dynamics in well-preserved and restored calcareous xerothermic grasslands (South Poland). *Biologia*, **59**, 447–456.

Bakker, J. P., Olff, J. H. Willems, Zobel, M. (1996). Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.*, **7** (2), 147–156.

Block, W. M., Franklin, A. B., Ward, J. P., Ganey, J. L., White, G. C. (2001). Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restor. Ecol.*, **9** (3), 293–303.

Chytrý, M., Sedláková, I., Tichý, L. (2001). Species richness and species turnover in a successional heathland. *Appl. Veg. Sci.*, **4**, 89–96.

Eberhards, G., Saltupe, B. (2000). Geological history, relief and deposits of the Lake Engures (Engure) area along the Baltic Sea. *Proc. Latvian Acad. Sci. Sect. B*, **54** (5/6) 141–147.

Ellenberg, H. (1996). *Vegetation Mitteleuropas mit den Alpen*. Stuttgart: Ulmer. 1095 pp.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulißen, D. (1992). *Zeigerwerte von Pflanzen in Mitteleuropa*. Göttingen: Verlag Erich Goltze KG. 258 pp.

Gaston, K. J., Evans, K. L., Lennon, J. J. (2007). The scaling of spatial turnover: Pruning the sicket. In: Storch D., Marquet P. A., Brown J. H. (eds.). *Scaling Biodiversity* (pp. 181–222). Cambridge: Cambridge University Press.

Gavrilova, G., Baroniņa, V. (2000). Vascular plant flora of the Lake Engures (Engure) drainage basin, Latvia, and the coastal zone of the Gulf of Riga. *Proc. Latvian Acad. Sci. Sect. B*, **54** (5/6) 177–189.

Gavrilova, Ģ., Šulcs, V. (1999). *Latvijas vaskulāro augu flora. Taksonu saraksts* [Flora of Vascular Plants of Latvia. List of taxa]. Rīga: Latvijas Akadēmiskā bibliotēka.136 pp. (in Latvian).

Gavrilova, G., Laiviņš, M., Priede, A., Medene, A. (2011). Alien flora in the Lake Engure Nature Park. *Proc. Latvian Acad. Sci. Sect. B*, **65** (5/6) 154–163.

Glenn-Lewin, D. C., van der Maarel, E. (1992). Patterns and processes of vegetation dynamics. In: Glenn-Lewin D. C., Peet R. K., Veblen T. T. (eds.). *Plant Succession. Theory and Prediction* (pp. 11–59). Population and Community Biology Series 11, Chapman & Hall.

Grime, J. P. (2002). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Chichester: John Wiley & Sons. 417 pp.

Grootjans, A. P., Hartog, P. S., Fresco, L. F. M., Esselink, H. (1991). Succession and fluctuation in a wet dune slack in relation to hydrological changes. *J. Veg. Sci.,* **2**, 545–554.

Heinrichs, S., Schulte, U., Schmidt, W. (2011). Eisbruch im Buchenwald — Untersuchungen zur Vegetationsdynamik der Naturwaldzelle „Ochsenberg" (Eggegebirge/Nordrhein-Westfalen). *Tuexenia*, **32**, 7–29.

Kent, M., Coker, P. (1994). *Vegetation Description and Analysis. A Practical Approach*. England: John Wiley & Sons. 363 pp.

Ketner-Oostra, R., Sykora, K. (2000). Vegetation succession and lichen diversity on dry coastal calcium-poor dunes and the impact of management experiments. *J. Coastal Conserv.,* **6** (2), 191–206.

Ketner-Oostra, R., Aptroot, A., Jungerius, P. D., Sykora, K. V. (2012). Vegetation succession and habitat restoration in Dutch lichen-rich inland drift sands. *Tuexenia*, **32**, 245–268.

Kļaviņš, M., Kokorīte, I., Rodinovs, V., Avotniece, Z., Spriņģe, G., Briede, A. (2011). Hydrometeorological parameters and aquatic chemistry of Lake Engure: Trends of changes due to human impact and natural variability. *Proc. Latvian Acad. Sci. Sect. B*, **65** (5/6) 138–145.

Kollmann, J., Rasmussen, K. (2012). Succession of a degraded bog in NE Denmark over 164 years — monitoring one of the earliest restoration eksperiments. *Tuexenia*, **32**, 67–85.

Krieger, A., Porembski, S., Barthlott, W. (2003). Temporal dynamics of an ephemeral plant community: Species turnover in seasonal rock pools on Ivorian inselbergs. *Plant Ecol.*, **167**, 283–292.

Kuiters, A. T. (2013). Diversity — stability relationships in plant communities of contrasting habitats. *J. Veg. Sci.*, **24**, 453–462.

Laime, B. (2000). Seashore plant communities of the Lake Engures (Engure) Nature Park, Latvia. *Proc. Latvian Acad. Sci. Sect. B*, **54** (5/6) 190–196.

Laiviņš, M., Gavrilova, Ģ. (2009). Biogeographic analysis of vascular flora in Ventspils and Daugavpils cities. *Latvijas Veģetācija*, **18**, 25–64.

Laiviņš, M., Rūsiņa, S., Frolova, M., Lyulko, I. (2007). Pine forest vegetation dynamics at ICP IM sites in Latvia. In: Kleemola, S., Forsius, M (eds.). *16th Annual Report 2007. UNECE Convention on Long-range Transboundary Air Pollution. International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems.* Helsinki: Finnish Environment Institute. *The Finnish Environment*, **26**, 37–54.

Laska, G. (2001). The disturbance and vegetation dynamics: A review and an alternative framework. *Plant Ecol.*, **157**, 77–99.

Magurran, A. E. (2007). Species abundance distributions over time. *Ecol. Letters,* **10**, 347–354.

Magurran, A. E. (2010). Diversity over time. *Folia Geobot.*, **43** (3), 319–327.

Magurran, A.E., Bailie, S. R., Buckland, S. T., Dick, J. M, Elston, D. A., Scott, E. M., Smith, R. I., Somerfiels, P. J., Watt, A. D. (2010). Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time (Review). *Trends Ecol. Evol.,* **25** (10), 574–582.

McCune, B., Grace, B. J. B. (2002). *Analysis of Ecological Communities*. Oregan: MjM Software Design, Gleneden Beach. 211 pp.

McCune, B., Mefford, M. J. (1999). *PC-ORD. Multivariate Analysis of Ecological Data, Version 4.0.* Oregon: MjM Software Design, Gleneden Beach. 237 pp.

Melecis, V. (2011). Project on development of a conceptual integrated model of socioeconomic biodiversity pressures, drivers and impacts for the long-term socioecological research platform of Latvia. *Proc. Latvian Acad. Sci. Sect. B*, **65** (5/6), 206–212.

Melecis, V., Karpa, A., Spuņģis, V. (2000). Assessment of the strategy used for insect population monitoring in the Lake engures (Engure) Nature Park, Latvia. *Proc. Latvian Acad. Sci. Sect. B*, **54** (5/6), 197–202.

Milberg, P., Hansson, M. L. (1993). Soil seed bank and species turnover in a limestone grassland. *J. Veg. Sci.,* **4**, 35–42.

Ozinga, W.A., Schaminée, J. H. J., van Groenendael, J. M. (2007). Long-term changes in species composition in the Netherlands in response to changing land-use. *New Zealand: New Home; New Habitat! New Idea? 49th Annual Conference of the International Association for Vegetation Science*. New Zealand: Palmerston North.

Pärtel, M., Zobel, M. (1995). Small-scale dynamics and species richness in successional alvar plant communities. *Ecography*, **18**, 83–90.

Preston, F.W. (1960). Time and space and the variation of species. *Ecology*, **41**, 612–627.

Rodwell, J. S., Schaminee, J. H. J., Mucina, L., Pignatti, S., Dring, J., Moss, D. (2003). The diversity of European vegetation. National Reference Centre for Agriculture, Nature and Fisheries, Wageningen. 168 pp.

Rosenzweig, M. L. (1995). *Species Diversity in Space and Time.* Cambridge: Cambridge University Press. 434 pp.

Russell, G. J. (1998). Turnover dynamics across ecological and geological scales. In.: McKinney, M. L., Drake, J. A. (eds.). *Biodiversity Dynamics. Turnover of Populations, Taxa and Communities* (pp. 377–404). New York: Columbia University Press.

Shurin, J. B. (2007). How is diversity related to species turnover through time? *Oikos*, **116**, 957–965.

Sival, F. P., Grootjans, A. P., Stuyfzand, P. J., Verschoore de la Houssaye, T. (1997). Variation in groundwater composition and decalcification depth in a dune slack: Effects on basiphilous vegetation. *J. Coastal Conserv.,* **3** (1), 79–86.

Smits, N. A. C., Schaminee, J. H. J., van Duuren, L. (2002). 70 years of permanent plot research in the Netherlands. *Appl. Veg. Sci.,* **5**, 121–126.

Süss, K., Storm, C., Schwabe, A. (2010). Sukzessionslinien in basenreicher offener Sandvegetation des Binnenlandes: Ergebnisse aus Untersuchungen von Dauerbeobachtungsflächen. *Tuexenia,* **30**, 289–318.

Sýkora, K. V., van den Bogert, J. C. J. M., Berendse, F. (2004). Changes in soil and vegetation during dune slack succession. *J. Veg. Sci.*, **15**, 209–218.

van der Maarel, E. (1988). Species diversity in plant communities in relation to structure and dynamics. In: During, H. J., Werger, M. J. A., Willems J. H. (eds.). *Diversity and Pattern in Plant Communities* (pp. 1–14). The Hague: SPB Academic Publishing.

van der Maarel, E., Sykes, M. T. (1993). Small-scale plant species turnover in a limestone grassland: The carousel model and some comments on the niche concept. *J. Veg. Sci.*, **4**, 179–188.

Vīksne, J. (1997). *Engure – putnu ezers* [Engure – Lake of Birds]. Rīga: Jāņa sēta. 225 pp. (in Latvian).

White, E. P., Adler, P. B., Lauenroth, W. K., Gill, R. A., Greenberg, D., Kaufman, D. M., Rassweiler, A., Rusak, J. A., Smith, M. D., Steinbeck, J. R., Waide, R. B., Yao, J. (2006). A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, **112**, 185–195.

White, E. P., Gilchrist, M. A. (2007). Effects of population-level aggregation, autocorrelation, and interspecific association on the species–time relationship in two desert communities. *Evol. Ecol. Res.*, **9**, 1329–1347.

Willems, J. H., van Deft, J. M. E., Rijke, M. K. (1981). Observations on north-west European limestone grassland communities. IV. Phytosociological notes on chalk grasslands in Denmark. *Folia Geobot. Phytotax.,* **16**, 391–406.

SUGU APRITE LAIKĀ UN AUGU SABIEDRĪBU DINAMIKA ENGURES EZERA DABAS PARKA BIOTOPOS

Veģetācijas dinamikas izpētē reti ir gadījumi, kad monitoringu vienlaicīgi veic vairākās atšķirīgās ekosistēmās. Tomēr šāda veida pētījumi ļauj padziļināti izprast veģetācijas struktūras un pazīmju izmaiņu mehānismus. Šajā pētījumā aplūkotas lakstaugu stāva izmaiņas, sugu aprite un sugu skaita–laika attiecība dažādu biotopu griezumā 12 gadu periodā ILTER monitoringa stacijā Engures ezera dabas parkā. Sugu aprite laikā definēta kā atšķirība sugu sastāvā starp diviem laika periodiem. Sugu skaita–laika attiecība tika novērtēta, izmantojot slīdošo logu pieeju. Detrendētā korespondentanalīze izmantota, lai noskaidrotu ikgadējās izmaiņas sugu sastāvā. Sugu skaits un kumulatīvais skaits, kā arī daudzveidība izteiktāk mainījās sugām bagātākajos nemeža biotopos, bet mazāk – meža biotopos. Sugu aprite stipri atšķiras starp biotopiem, un tā nebija saistīta ar biotopu stabilitāti, kā tas konstatēts citos līdzīgos pētījumos. Sugu skaita–laika attiecība sešos biotopos bija stipri zemāka, nekā minēts līdz šim publicētos pētījumos. Tas varētu būt skaidrojams ar kopējo platuma grādu sugu daudzveidības gradientu, jo līdzšinējie pētījumi veikti galvenokārt zemajos platuma grādos, bet šajā pētījumā apskatītie biotopi reprezentē boreālo zonu. Augstajos platuma grādos gan sugu daudzveidība, gan aprite ir zemāka nekā zemajos platuma grādos. Veģetācijas dinamika nabadzīgā zālājā skābā augsnē, starpkāpu ieplakā, zāļu purvā un kāpu mežā interpretējama kā fluktuācijas. Sausā un mitrā mežā un piejūras zālājā bija novērojamas veģetācijas virzītas izmaiņas jeb sukcesija (attiecīgi — kserofitizācija, sugu sastāva nomaiņa un aizaugšana). Pludmales veģetācijas izmaiņas konstatētas gan dabiskas sukcesijas pazīmes (veģetācijas saslēgšanās), gan antropogēni izraisītu fluktuāciju pazīmes.

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