

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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157

TSIPE AAVIK

Plant species richness,
composition and functional trait pattern
in agricultural landscapes –
the role of land use intensity and
landscape structure



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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

- I** Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., Billeter, R., Bukacek, R., Burel, F., De Blust, G., De Cock, R., Dirksen, J., Edwards, P. J., Hamersky, R., Herzog, F., Klotz, S., Kühn, I., Le Coeur, D., Miklova, P., Roubalova, M., Schweiger, O., Smulders, M. J. M., van Wingerden, W. K. R. E., Bugter, R. & Zobel, M. 2008. Plant functional group composition and large-scale species richness in the agricultural landscapes of Europe. *Journal of Vegetation Science* 19: 3–14.
doi:10.3170/2007-8-18308
- II** Aavik, T., Augenstein, I., Bailey, D., Herzog, F., Zobel, M. & Liira, J. 2008. What is the role of local landscape structure in the vegetation composition of field boundaries? *Applied Vegetation Science* 11: 375–386.
doi:10.3170/2008-7-18486
- III** Aavik, T. & Liira, J. 2009. Agrotolerant and high nature-value species – plant biodiversity indicator groups in agroecosystems. *Ecological Indicators* 9: 892–901. doi:10.1016/j.ecolind.2008.10.006
- IV** Aavik, T. & Liira, J. Quantifying the effect of agricultural land use intensity, habitat properties and landscape structure on the vegetation of field boundaries (submitted manuscript)

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Author's contribution to the papers:

	I	II	III	IV
Original idea		*	*	*
Study design				*
Data collection	*	*	*	*
Data analysis		*	*	*
Manuscript preparation	*	*	*	*

I. INTRODUCTION

Transition from traditional agricultural activities to intensive land use practises during the last century has resulted in drastic changes in the environmental conditions of agricultural landscapes (Tilman et al. 2001; Green et al. 2005; Liira et al. 2008). This has been associated with a steep decline in the biodiversity of agroecosystems, a corresponding simplification of communities and a loss of ecosystem services (Swift et al. 1996; Stuart Chapin III et al. 2000; Stoate et al. 2001; Foley et al. 2005). It has been demonstrated that the decline of biodiversity in agricultural landscapes is affected mostly by the intensification of agricultural land use (Kleijn et al. 2009) and by extensive changes in landscape structure (Fahrig 2003; Kivinen et al. 2009).

Agricultural land use intensity threatens the environmental quality of natural and semi-natural habitats in agricultural landscapes via leaching of fertilisers and herbicides from adjacent fields (Kleijn & Snoeijing 1997; de Snoo & Van der Poll 1999). Enhanced nitrogen and phosphorus concentrations facilitate the growth of competitive perennials and fast-growing ruderal plants, causing a decrease in species richness and changes in species and functional composition (Kleijn & Snoeijing 1997; Marshall & Moonen 2002). Therefore, it has been suggested that organic farming or environmentally friendly management may improve the environmental conditions of the habitats neighbouring agricultural field (Bengtsson et al. 2005; Kleijn et al. 2006; Gibson et al. 2007). However, the alarming reports show that the schemes that have been implemented to protect the agroecosystem biodiversity may not be effective (Kleijn et al. 2001), which indicates that there is still a lack of ecological insight into the processes affecting agroecosystem diversity.

In addition to agricultural land use intensification, changes in landscape structure explain a large proportion of variation in plant species diversity and composition in agricultural landscapes. The decline in habitat area and the loss of habitat heterogeneity have been demonstrated to impose major pressure on biodiversity (Benton et al. 2003; Fahrig 2003). Beside the direct effect of the availability and diversity of habitats, large habitat patches also buffer the influence of agrochemicals in the core area of patches and provide suitable ecological conditions for habitat specialist species (Burel et al. 1998). In addition, habitat connectivity and proximity affects the vegetation composition as the cohesion between habitats influences the dispersal success of species between suitable habitats (Geertsema et al. 2002; Petit et al. 2004).

Different linear elements bordering agricultural fields (such as hedgerows, road verges, ditch verges and forest edges) and small area patches of natural and semi-natural vegetation (such as stone piles and small woodlots) cover a significant area in agricultural landscapes. These elements have been considered to be the key habitats for maintaining biodiversity in contemporary agroecosystems: on the one hand, field boundaries can themselves serve a habitat function; on the other hand, field boundaries may connect fragmented (semi-)natural patches into an integrated functional network that enables

dispersal between suitable habitat patches for several species. Therefore, such a cohesive network of field boundaries together with natural and semi-natural habitat patches being referred to as green veining (Grashof-Bokdam & van Langevelde 2005) has been suggested to compensate for the negative effects of high intensity agricultural land use and habitat fragmentation (Le Coeur et al. 2002; Marshall & Moonen 2002; Fahrig 2003).

Likewise the biodiversity in habitat patches, the biodiversity in boundary habitats may be seriously altered by factors related to land use intensity. Furthermore, due to the narrow and linear structure of field boundaries the negative effects of these factors are probably even more pronounced. The “life belt” function of field boundaries in biodiversity conservation may thus be rather negligible and thorough research is needed to clarify which conditions could improve the habitat and dispersal corridor function of field boundaries. For an effective maintenance of field boundary vegetation it is also essential to elucidate the role of different agri-environmental support schemes and to advance the management methods according to the ecologically reasoned suggestions. However, the knowledge on the influence of such schemes on the boundary vegetation has remained rather scarce and the results of studies focussing on this question are controversial. For example, the impact of organic farming, which is one of the most widespread agri-environment methods, has been most evident on weed diversity in agricultural fields (Hole et al. 2005; Gabriel et al. 2006; Gibson et al. 2007), while the positive effect of organic farming on the vegetation of field boundaries has been less apparent (Clough et al. 2007; Gibson et al. 2007).

Small-scale structural features may largely determine the environmental conditions and hence the vegetation composition in field boundaries. For instance, the presence of tree and shrub layer may provide suitable conditions for shade-tolerant species (Petit et al. 2004; Boutin et al. 2008). Regularly mown road verges and field boundaries may compensate the habitat loss for species characteristic of semi-natural grasslands (Hovd & Skogen 2005; Cousins 2006). Drainage ditches enable the growth of moisture-demanding species (Milsom et al. 2004). Most of these studies on field boundary vegetation have usually addressed only one of the structural aspects, i.e. hedgerows (Aude et al. 2004; Deckers et al. 2004), ditches (Milsom et al. 2004; Manhoudt et al. 2007; Blomqvist et al. 2008) or road verges (Hovd & Skogen 2005; Cousins 2006), while comparative studies on different types of field boundaries have been rare (Freemark et al. 2002). Furthermore, the fact that field boundaries usually encompass more than one structural feature has mostly been neglected. For example, the vegetation composition of ditch verges has been shown to depend on the presence or absence of trees or shrub layers (Le Coeur et al. 1997).

The question of the relative importance of landscape- and local-scale factors of habitat structure on the biodiversity of green veining elements compared to farming practices has not yet received a comprehensive answer. One of the reasons is the frequent correlation between the variables of land use and

landscape structure (Bengtsson et al. 2005; Grashof-Bokdam & van Langevelde 2005; Norton et al. 2009), which makes it difficult to distinguish whether the variation in diversity and composition is caused by management intensity or landscape properties. Furthermore, studies on biodiversity in agricultural landscapes have focused typically either on individual landscape elements or on a single farm, while fewer studies address the impact of surrounding landscape configuration on plant diversity (Grashof-Bokdam & van Langevelde 2005).

The use of appropriate indicators is another significant aspect in the adequate estimation of the effect of land use intensity and landscape structure. Species richness, one of the most exploited biodiversity indicators (Büchs 2003; Clergue et al. 2005; Gibson et al. 2007), provides us with insufficient information on qualitative changes. The rare or Red List species have been recommended as indicators of habitat quality (Zechmeister & Moser 2001; Weibull & Östman 2003; Clergue et al. 2005), but such an approach does not seem to be very practical as contemporary agroecosystems seldom host rarities (Kleijn et al. 2006). The specific response of vegetation to land use and landscape structure depends on the traits of species, most of all on their dispersal ability, seed persistence, life span and tolerance to frequent disturbances (Dupré & Ehrlen 2002; Geertsema et al. 2002; Jacquemyn et al. 2003). The evaluation of the reaction of every individual species is, however, too labour-intensive, and the obtained information is too detailed to enable drawing conclusions about the general trends of biodiversity. Therefore, the analysis of plant trait patterns and the representation of functional types in communities have been suggested in order to provide more generalized qualitative information on the changes in vegetation (Lavorel et al. 1997; Diaz et al. 2007).

The correlation of plant traits to management intensity and landscape structure has provided a basis for classifying species into emergent groups, e.g. indicator species (Mitchley & Xofis 2005; Liira et al. 2007), various ecological strategy types (Grime 1977) and hemeroby types (Jalas 1955; Hill et al. 2002). Other simple classifications of species into broad response groups have been proposed, such as habitat generalists or matrix species vs habitat specialists, weeds or ruderals vs species of conservation value (Cook et al. 2002; Dupré & Ehrlen 2002; Adriaens et al. 2006) and nature quality groups (van Strien et al. 1989; Smart et al. 2006). Although the use of broadly identified plant functional types may conceal the detailed mechanisms that underlie the response of species to environmental or anthropogenic factors, the *ad hoc* groups are most promising in addressing the variation of general plant communities, i.e. at landscape or global scales (Diaz et al. 2004; Kahmen & Poschlod 2008). However, they still have not been applied frequently in monitoring systems and environmental assessments (Godefroid & Koedam 2003; Smart et al. 2006; Van Cauwenbergh et al. 2007).

The assessment of biodiversity in more practical applications, e.g. the monitoring of the influence of organic farming and agri-environmental schemes, should be relatively simple and little time-consuming on the one hand, but

should also reflect the qualitative response of species to land use intensity and landscape structure on the other. In addition, the biodiversity indicators should also consider the regional specificity of a species pool (Waldhardt et al. 2003). Yet, the task to unify these simple qualities into one indicator is not easy. One straightforward approach to evaluate the trends in plant diversity is to measure the presence-absence frequency of species in agricultural fields, and based on that classify them into response groups characterised by different tolerance to agricultural disturbance. One may assume that species frequent in agricultural fields will probably perform successfully also in agricultural landscapes even when the amount of green veining habitats is negligible. All other species that are rare or absent in agricultural fields, depend on the availability of natural and semi-natural green veining habitats and do not tolerate high agricultural disturbance. These species could consequently be defined as high nature-value species from the point of view of agricultural land use. The abundant occurrence and diversity of agrotolerant species in the landscape is expected to be positively related to agricultural intensification, and to the loss of natural and semi-natural habitats, while the high diversity of nature-value species would indicate positive processes in agricultural landscapes for habitat specialist and hemerophobic species (**III**, Fig. 1).

The objectives of the thesis were as follows:

- 1) To analyse the relative impact of large-scale landscape structure and agricultural land use intensity on plants species richness, composition and functional trait pattern in the green veining elements of agricultural landscapes (**I, III, IV**);
- 2) To detect which plant functional traits respond to agricultural disturbances most clearly (**I**);
- 3) To specify the support function of field boundaries in maintaining the plant diversity of agroecosystems (**II, III, IV**);
- 4) To elucidate the role of field boundary structure on the vegetation of field boundaries (**II, III, IV**);
- 5) To improve the methodology for monitoring biodiversity in agricultural landscapes by developing indicators for the evaluation of plant diversity (**I, III, IV**).

2. MATERIAL AND METHODS

2.1. Study sites

The study of paper **I** was part of the European Union research project “Greenveins”. The aim of the project was to detect the relationship between biodiversity, landscape structure and land use intensity in temperate Europe. We used 25 agricultural landscape study sites representing combined gradients of land use intensity and landscape structure in Europe. The 4 x 4 km landscape study sites were distributed over seven countries across temperate Europe: France, Belgium, The Netherlands, Germany, Switzerland, the Czech Republic and Estonia (three or four study areas per country). The methodological framework of papers **II** and **III** followed the study design principles of “Greenveins” project with the exception that only Estonian data were used.

In paper **IV**, the methodology was developed in relation to European Science Foundation project “Agripopes”, but we included also suitable data from the “Greenveins” dataset. The study was carried out on 42 farms of Tartu County in Estonia covering an area of approximately 30 x 50 km.

2.2. Vegetation data

In studies **I-III**, about 240 2 x 2 m plant sampling plots per landscape study site (4 x 4 km) were located randomly in three types of landscape elements: agricultural fields, linear semi-natural landscape elements (field boundaries) and semi-natural and natural habitat patches (grasslands and forests) with a predetermined ratio (1:5:4 respectively to arable:linear:patch elements). In paper **II**, only the data from field boundaries and fields were used. Large-scale plant diversity in each landscape study site was estimated by pooling species lists of these 2 x 2 m survey plots (papers **I** and **III**). In paper **IV**, the field boundary vegetation in 313 plots with a size of 2 x 2 m was recorded. The number of sample plots per farm varied proportionally according to farm size.

The classification of each species according to their functional traits in paper **I** was made with the help of the trait database BIOLFLOR (Klotz et al. 2002). Based on BIOLFLOR data, we included two additional functional group classifications combining the traits characterising species invasiveness, hemeroby and tolerance to disturbance: “nature quality indicator” classes (high vs low nature quality species) and “ecological flexibility” of species.

In paper **II**, plant species were assigned Ellenberg ecological indicator values of light, soil fertility and moisture (Ellenberg et al. 1991).

In papers **III** and **IV**, the target of the analyses was to assess the plant diversity of green veining habitats taking into account species agrotolerance. Information on in-field flora (i.e. sampling plots in agricultural fields) was used

to classify species into the emergent group of agrotolerant species. The classification was applied on vegetation data from green veining elements. We defined a plant species to be agrotolerant if its presence frequency in the sample plots of agricultural fields was 10% or more. All other plant species were classified as nature-value species including rare weeds and hemerophytic species.

2.3. Data on landscape structure and land use intensity

The habitat composition of landscape study sites was mapped from aerial photographs (**I**, cf. (Bailey et al. 2007)) or using the Estonian Basic Map and Cadastral Map (**II**, **III**, **IV**). In studies **I-III**, landscape parameters were calculated for 4 x 4 km landscapes. In paper **IV**, the large-scale landscape structure was evaluated within a circle-shaped landscape window with a radius of 250 meters around the vegetation sampling plot. Landscape elements were classified into broad classes, such as forests, grasslands, roads, non-greenvein habitats and their boundaries. For vegetation plots in field boundaries and other green veining elements, the small-scale structural features in the landscape (the presence/absence of ditches and roads) and the vertical structure of a habitat (the presence/absence of trees or shrubs) within a 10 m radius from the centre of the vegetation plot were recorded during fieldwork (**II**, **III**, **IV**). In paper **IV**, the field boundary width was also recorded.

Indices of agricultural land use intensity in papers **I-III** were adopted from standardised interviews with approximately ten farmers or land managers within each landscape study site (Herzog et al. 2006). In paper **IV**, the categorical factor of organic and conventional farming was used as a proxy for land use intensity.

2.4. Data analyses

Partial principal component analysis (pPCA) was used to analyse the functional group composition and abundance within functional groups in relation to the parameters of land use intensity and landscape structure, conditioning on geographical location and country (**I**). Partial canonical correspondence analysis (pCCA) was applied in order to determine the relative influence of landscape structure, land use and habitat properties on the species composition of field boundaries (**IV**) (Ter Braak & Šmilauer 2002). The analyses were carried out in PC-Ord ver. 5.10 (McCune & Grace 2002) and CANOCO ver 4.5.

Multi-response permutation procedures (MRPP) were used to determine the distinctness of species composition among field boundaries with different habitat structure (**II**, **IV**). Detrended Correspondence Analysis (DCA) was performed in order to illustrate the variation of plant species composition in

field boundaries (**II**, **IV**). Indicator species analysis was used to detect species typical of field boundaries with different habitat structure (**II**). DCA, MRPP and indicator species analysis were carried out using PC-Ord ver. 5.10 (McCune & Grace 2002).

The response of landscape-scale plant species richness within plant functional groups to the gradients of landscape structure and land use intensity in study **I** was investigated using general linear mixed modelling (proc MIXED, in SAS ver 9.1). The first general linear mixed model focused on the determinants of species richness within five growth forms: pteridophytes, legumes, other forbs (*sensu stricto*), grasses and sedges. In the two following models we focused on nature quality indicator classification (high vs low) and life-span types (annual vs perennial), conditioning on growth form (*sensu lato*, graminoids and forbs).

In studies **III** and **IV**, General Linear Mixed Models (GLMM) were used to analyse the impact of land use and landscape structure on plant species richness within the groups of agrotolerant and nature-value species applying a repeated measures design to take into account the fact that species were sampled in the same plots (**III**, **IV**). Stepwise procedure was applied to find the optimal set of statistically significant metrics of land use and landscape structure affecting the species diversity. Analyses were carried out in SAS ver. 9.1 (Littell et al. 1996).

3. RESULTS

3.1. The plant functional composition of agricultural landscapes

The results of the pPCA in study **I** demonstrated that there was a clear shift from low nature quality plant species, exotics, urbanophilic and R-strategy plants to the dominance of high nature quality species, C- and S-strategy plants as the land use intensity of landscapes decreased and habitat availability increased (**I**, Fig. 1). This major transition in the functional composition of vegetation was also illustrated by shifts from the dominance of annuals and selfing species to the dominance of perennials, and from seed dispersed species to clonal type vegetative dispersal (**I**, Fig. 1). The second axis of pPCA reflected the transition from the dominance of forbs and sedges to the dominance of grasses, from erosulate species to hemirosette or rosette species, and from the prevalence of insect-pollinated species to species with abiotic pollen vectors.

3.2. The species composition of field boundaries

In study **II**, which encompassed study sites from all over the Estonian mainland, a total of 384 vascular plant species were recorded in field boundaries. In study **IV**, which included study sites only from Tartu County, 237 plant species were registered. The most frequent species in field boundaries were common generalist species being often present in arable fields as well (*Taraxacum officinale*, *Elymus repens*, *Cirsium arvense* and *Phleum pratense*), while only a few rare and protected species were registered (e.g. *Dactylorhiza fuchsii*, *Dactylorhiza maculata* and *Epipactis helleborine*).

MRPP and DCA ordination analyses revealed that field boundary structure was one of the main factors affecting species composition: the vegetation composition in field boundaries adjacent to road, grassland, ditch and woody field boundaries were significantly distinct from one another (**IV**, Fig. 2a). Furthermore, the results of paper **II** (Fig. 3) suggest that even finer classification of field boundary types may be necessary to detect the response of vegetation composition to local habitat structure: (1) joint boundary type of grassy field boundaries, road verges, woody road verges and road verges adjacent to ditches into one class; (2) ditch verges; (3) woody boundaries; (4) woody ditch verges; (5) woody ditch verges adjacent to roads.

Indicator species analysis revealed that boundaries adjacent to road verges and grasslands were characterised by species typical of open and disturbed habitats: e.g. *Taraxacum officinale*, *Achillea millefolium*, *Artemisia vulgaris*, *Plantago major* and *Poa annua*; or weed species *Capsella bursa-pastoris* and *Matricaria perforata* (**II**, Table 3). The herb layer of woody boundaries (forest edges, tree-lines, hedgerows) was characterised by shade-tolerant and nitrophilous species such as *Rubus idaeus*, *Elymus repens* and *Urtica dioica*. The list

of characteristic species of ditch verges included species typical of semi-natural grasslands such as *Centaurea jacea*, *Galium boreale* and *Ranunculus acris*, and species characteristic of moist and nutrient-rich soils such as *Filipendula ulmaria*, *Geranium palustre*, *Aegopodium podagraria* and *Angelica sylvestris*. Several species were generalists occurring frequently in almost all types of field boundaries, e.g. *Phleum pratense*, *Vicia cracca*, *Festuca pratensis*, *Poa pratensis* and *P. trivialis* (**II**, Table 3).

In addition to local boundary structure, large-scale landscape structure accounted for a considerable amount of the variation in field boundary species composition. The availability of natural and semi-natural habitats in the landscape study site (4 x 4 km) was correlated with the largest variation in species composition (**II**, Fig 3–4). The results of variance partitioning in study **IV** (Fig. 1) revealed that the parameters of landscape structure in the surrounding of the vegetation plot (within a radius of 250 meters) accounted for the largest proportion of variation in species composition.

The variation in species composition was also correlated with the Ellenberg indicator value of soil fertility and average amount of inorganic N-fertilisers (**II**, Fig. 2–3) indicating an influence of land use intensity on plant species composition. In contrast, the variation partitioning in study **IV** (Fig. 1) revealed that only very low amount of variation in species composition was explained by farming type (organic and conventional).

3.3. Landscape-scale species richness

The greater availability of natural and semi-natural habitats in a landscape increased the landscape-scale species richness within all growth forms (grasses, legumes, sedges, pteridophytes and other forbs) (**I**, Fig. 2a), while land use intensity, characterised by crop diversity in the model, decreased the species richness of two growth forms – sedges and pteridophytes (**I**, Fig. 2b).

Similarly to the effect on the species richness within growth forms, the higher proportion of natural and semi-natural habitats had a positive effect on the high nature quality species richness of forbs and graminoids (**I**, Fig. 3a). The increased density of edge habitats in the landscape resulted in remarkably decreased species richness of the high nature quality group, and a slight increase in low nature quality species richness. Land use intensity was negatively related to the landscape-scale species richness of the high nature quality group, and positively to the richness of the low nature quality group (**I**, Fig. 3b).

The number of habitats per landscape had a positive effect on the species richness within all life-span groups, while the positive effect of habitat availability was evident only for perennial forbs (**I**, Fig. 4a). A significant negative relationship between the mean habitat patch size and large-scale species richness was observed only in the functional group of annual graminoids (**I**, Fig. 4b). The increasing number of crops caused an increase in the richness of annuals and a decrease in the richness of perennials (**I**, Fig. 4c).

The analysis of landscape-scale species richness (i.e. gamma-diversity) in relation to the variables of landscape structure and land use intensity revealed that the proportion of natural and semi-natural habitats in a landscape is a single sufficient predictor of large-scale species richness, while none of the other variables of landscape or land use intensity improved the model (**III**, Fig. 3).

3.4. Small-scale species richness

Small-scale species richness was analysed within two agrotolerance groups – agrotolerant species and nature-value species. The results of studies **III** and **IV** suggest that land use is a significant predictor of small-scale species richness. The model of species richness in study **III** revealed that higher average nitrogen fertilisation in a landscape affects negatively both nature-value and agrotolerant species (**III**, Table 3). A particularly strong negative effect of nitrogen fertilisation was observed in field boundaries, where the decrease in species richness was approximately eight times stronger than in the core area of woodlands or semi-natural grasslands. The results of study **IV** revealed that organic farming significantly increases species richness in field boundaries. The effect was, however, group-specific as organic farming only enhanced the species richness of nature-value species, whereas the richness of agrotolerant species did not depend on management intensity (**IV**, Fig. 3).

The availability of natural and semi-natural habitats in a landscape (4 x 4 km) had a significant effect on small-scale species richness (**III**, Table 3). The higher percentage of woody habitats enhanced species richness in both species groups, but the effect was twice as strong for nature-value species. The significant interaction between the proportion of herbaceous habitats and the adjacency of agricultural land revealed that the higher percentage of herbaceous semi-natural habitats in a landscape enhanced species richness in field boundaries. In paper **IV**, however, we did not detect any relationship between the surrounding landscape structure ($r = 250$ m) and small-scale species richness.

In both studies **III** and **IV**, we found that local boundary structure played a significant role in determining species richness, but the effect was in several cases very species-group specific. For example, ditches enhanced the species richness only of nature-value species (**III**, Fig. 4d; **IV**, Fig. 5a), while woody layer suppressed agrotolerant species (**III**, Fig. 4c; **IV**, Fig. 5b). Road verges had a positive effect on the species richness of agrotolerants in study **III** (Fig. 4b) and on both species groups in study **IV** (Fig. 4a).

The width of the field boundary was critical for nature-value species, but only in open boundaries (**IV**, Fig. 6a). At the same time, the species richness of agrotolerant species decreased in wider open field boundaries (**IV**, Fig. 6b). The results imply that effective boundary width for maintaining vegetation diversity starts from three to four meters, after which the number of agrotolerant species significantly decreases and the richness of nature-value species levels off.

4. DISCUSSION

Modelling efforts indicate that habitat loss together with the deterioration of habitat quality may be the main drivers of biodiversity decline on a large scale (Sala et al. 2000). Although some empirical data exist, information on the impact of landscape-scale processes on biodiversity covering large geographical range has still remained very scarce. The scale of such studies is one reason why it is difficult to consider the combined effects of land use intensity and landscape structure: studies on biodiversity in agricultural landscapes have focused typically either on individual landscape elements or on a single farm, while few studies address the impact of surrounding landscape configuration on plant diversity (Grashof-Bokdam & van Langevelde 2005). Another problem is that the effects of land use intensity and landscape properties are often not distinguished. One of the causes for this is the frequent correlation between the variables of land use and landscape structure (Bengtsson et al. 2005; Norton et al. 2009). In the present study we sampled the vegetation within a wide range of landscapes and different land use intensity, intending to retain the independence among those two factor groups as much as possible. This allowed us to extract the effects of landscape structure, land use intensity and local habitat characteristics on the plant functional and species diversity of agricultural landscapes.

The studies of the thesis imply that such simple measures as the landscape-scale proportion of natural and semi-natural habitats can be very effective predictors of plant functional trait patterns as well as species diversity of agricultural landscapes at various spatial scales and along wide geographical range (**I, III**). The abundance and composition of plant functional groups in European agricultural landscapes were correlated mainly to the combined gradient of natural habitat availability and agricultural land use intensity (**I**). The species richness within functional groups also showed a consistent relationship to the proportion of (semi-)natural habitats, particularly in case of habitat specialists, such as sedges, pteridophytes, perennial forbs and the species of high nature quality. The landscape-scale species richness in Estonian agricultural landscapes was affected positively by the total area of natural and semi-natural habitats (**III**). We suggest that since larger proportion of natural and semi-natural habitats indicates also to the potentially larger core area of habitat patches, the positive relationship between landscape-scale species diversity and percentage of green veining may reflect the availability of suitable environmental conditions for habitat specialist species. This hypothesis is also supported by the positive relationship between the small-scale richness of nature-value species and habitat availability in the landscape.

We found that increasing land use intensity had significant negative effects on the functional composition and species diversity of plants at different spatial scales (**I, III, IV**). Higher intensity in land use decreased the landscape-scale richness of perennial species and high nature quality species, and increased the richness of annuals and the species of low nature quality, i.e. species that are adapted to disturbed habitats (Kleijn & Verbeek 2000) (**I**). Landscape-scale

(III) as well as farm-scale (IV) land use intensity influenced the small-scale richness of field boundary vegetation. The negative impact of intensive agriculture and the positive effect of organic farming have been observed in a number of previous studies (Bengtsson et al. 2005; Kleijn et al. 2009). In addition, we found that the positive effect of organic farming was particularly apparent on the richness of nature-value species, while agrotolerant species remained unaffected regardless of management type. This implies that the boundaries of organic fields may support a higher diversity of hemerophobic and habitat specialist species (Manhoudt et al. 2007), while nitrophilous and disturbance-tolerant species can persist in the boundaries of all farming types. The latter may be the reason why farm management type explained only a small fraction of the variation in species composition and why plant assemblages were still floristically relatively similar in the boundaries of conventional and organic farms (IV).

It has been suggested that field boundaries such as road verges, tree-lines, hedgerows and ditch verges may compensate the loss of natural and semi-natural habitats (Marshall & Moonen 2002; Grashof-Bokdam & van Langevelde 2005). We found that landscapes with high densities of edges, on the contrary, suppressed the landscape-scale richness of high nature quality species (I). Furthermore, the flora of field boundaries had a large overlap with the flora of agricultural land in Estonian landscapes (II), indicating that field boundaries provide habitats mainly for generalists, weeds and disturbance-tolerant species, many of which can also be found on adjacent arable land. We also found that the habitat quality and thus the floristic composition and diversity of field boundaries may depend largely on the field boundary structure, notably the presence of road, ditch and tree layer (II, III, IV), the width of field boundary (IV) and adjacent land use intensity (III, IV).

The combinations of structural elements, i.e. trees, ditches and the vicinity of road, create a diversity of habitats that are suitable for species with different ecological requirements. The richness of nature-value and moisture-demanding species was significantly higher in the boundaries adjacent to ditches, implying that ditch verges with moderate management intensity and decreased use of agrochemicals near field margins can have high potential for maintaining plant diversity in agroecosystems (Musters et al. 2009). Road verges, on the other hand, supported the diversity of agrotolerant and light-demanding species. Indeed, road verges experience a relatively high rate of disturbance due to the intensive use of adjacent areas on both sides and frequent mowing. Mowing with moderate frequency generally has a positive effect on the vegetation diversity of boundaries (Schaffers 2002; Hovd & Skogen 2005). The excessively intensive mowing regime that is often practiced in road verges may cause a shift from perennial semi-natural vegetation to a prevalence of disturbance-tolerant and light-demanding opportunistic annuals and ruderals (Forman & Alexander 1998; Truscott et al. 2005), many of which belong to the group of agrotolerant species. However, wider road verges may encompass gradual decreases in disturbance and increases in moisture, and may thus still be

important habitats for a number species of semi-natural grasslands (Cousins 2006).

It has been shown that woody linear habitats may contribute to the diversity of forest plant species in agricultural landscapes (Petit et al. 2004; Boutin et al. 2008). Indeed, we recorded several characteristic forest species in forest edges, tree-lines or hedgerows (**II**). However, woody boundaries were also suitable for ruderal species preferring high soil nutrient content, which indicates agricultural disturbances and chemical pollution from neighbouring fields. In addition, the light and soil conditions of hedgerows differ from the conditions in woodland interior (McCollin et al. 2000) and the survival of woodland species is likely to be limited. The significance of woody field boundaries as habitats or dispersal corridors for forest species may therefore be frequently over-estimated.

There has been a debate whether or not wider field boundaries enhance small-scale plant diversity (Ma et al. 2002; Gibson et al. 2007). Our results did not confirm a relationship between general species richness and boundary width *per se* (**IV**). Nevertheless, a relationship became evident when we analysed the effect of boundary width separately on agrotolerant and nature-value species. The richness of nature-value species increased significantly with an increase in boundary width in open boundaries, while agrotolerant species prevailed in narrow field boundaries. As the area of semi-natural grasslands has decreased significantly during the 20th century (Poschlod & WallisDeVries 2002), more attention should be paid to potential refugium habitats that can offer environmental conditions similar to grasslands (Aavik et al. 2008). Several studies have demonstrated the role of open field boundaries as alternative habitats for grassland species (Smart et al. 2002; Cousins 2006). Our results imply that such boundaries should have a width of at least three to four meters to assure habitat quality for grassland species.

We showed that the distinction between agrotolerant and nature-value species based on simple observed frequency of species in fields or classification of species into high and low nature quality groups based on trait databases can reveal the divergent response of those indicator groups to land use intensity, landscape and habitat structure. This implies that general species richness is not an effective indicator of the state of biodiversity in agricultural landscapes and that addressing low nature quality/agrotolerant and high nature quality/nature-value species instead of total species richness will reveal more qualitative correlations and trends between biodiversity and its drivers. The contrasting reaction of species to land use intensity and landscape structure indicates that the response of agrotolerant species can even outbalance the response of nature-value species, and thus there is a danger of not detecting changes in analysing total species richness *per se*.

Nature-value and high nature quality species include specialists of natural and semi-natural habitats and hemerophytic species, but also rare weeds whose abundance has drastically decreased due to intensive agricultural methods. Therefore, the group of high nature-value indicator species should be the main concern of biodiversity conservation and a more adequate indicator of

environmental quality in agricultural landscapes. We admit, however, that an agrotolerant species in one study region may be considered a nature-value species and even a keystone of biodiversity in other parts of Europe. Therefore, every region should have its own characteristic list of agrotolerant and nature-value species (**II**, **III**, **IV**), or alternatively a rough estimate of nature-quality status (**I**) should be used in monitoring. The frequency-based flexible classification of species into such indicator groups seems to be more adequate as it takes into account regional aspects of land use history and species availability in the regional species pool, which is one of the most important prerequisites for an informative indicator.

5. CONCLUSIONS

The results of the thesis demonstrate that primarily local habitat structure, but also the structure of the surrounding landscape and land use intensity, all contribute to the plant species diversity and composition of agricultural landscapes. Furthermore, we showed that these factors, particularly the availability of natural and semi-natural habitats in the landscape, have an extensive impact on the diversity and distribution of plant functional trait composition. The loss of species in relation to habitat degradation concerns mostly those inhabiting undisturbed natural or semi-natural ecosystems, while disturbance-tolerant species predominate in highly fragmented agricultural landscapes. Increasing land use intensity and a decrease in the area of (semi-)natural habitats would likely benefit annuals, selfing species and species dispersing with seeds, while suppress perennial species and species with vegetative dispersal.

Contrary to our expectations, field boundaries supported mainly disturbance-tolerant and generalist species, and less habitat specialist and rare species. These findings challenge the idea that corridors and edge habitats may compensate the loss of natural and semi-natural communities for plant species of high nature-value. For the conservation of plant diversity, the protection of patch-mosaic systems consisting of historically continuous, natural and semi-natural habitats in agricultural landscapes seems to be far more important than the creation of narrow linear elements.

However, there was a high variation in the habitat quality of different field boundary types: boundaries related to ditches had a vegetation characteristic to semi-natural grasslands, whereas road verges offered habitat mainly for disturbance-tolerant species. Furthermore, we found that organic farming and lower fertilizer inputs in general may significantly improve the habitat quality of field boundaries, particularly for high nature-value indicator species. In addition, we suggest that the broadening of field boundaries with permanent vegetation to at least three to four meters is obligatory for creating appropriate habitat conditions for species that are more sensitive to agricultural disturbance. These results indicate that the conservation of wide permanent vegetation strips, the reduced use of agrochemicals near the field margins and regular mowing with moderate intensity may still notably enhance the conservation potential of field boundaries. Maintaining suitable environmental conditions and improving connectivity within the network of field boundaries and patches of (semi-)natural habitats will advance species conservation at landscape scale.

We suggest that addressing the local classification of agrotolerant and high nature-value indicator species in the evaluation of biodiversity in agricultural landscapes instead of total species richness will reveal more qualitative correlations and trends between biodiversity and its drivers. The contrasting reaction of species to biodiversity drivers in our studies implies that the response of agrotolerant species can even outbalance the response of nature-value indicator species, and thus there is a danger of not detecting changes in analysing total species richness *per se*.

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SUMMARY IN ESTONIAN

Maakasutuse ja maaстiku struktuuri мõju põllumajandusmaastike taimkatte mitmekesisusele, liigilisele koosseisule ja funktsionaalsele tunnuste mustriile

Üleminekuga intensiivsele põllumajandusele möödunud aastasajal on kaasnenud ulatuslikud muudatused maakasutuses ja maaстiku struktuuris. Põldude suurenemine, põllumajandusmasinate laialdane kasutuselevõtt ning väetiste ja teiste saagikust tõstvate toimeainete kasutamine – need on märksõnad, mis iseloomustavad 20. sajandil kogu Euroopas asetleidnud põllumajanduse intensiivistumise „võidukäiku“. Saagikust tõstvate meetodite kasutuselevõtt on põhjustanud märkimisväärset bioloogilise mitmekesisuse kahanemist. Kõige otsesem ohutegur on looduslike ja pool-looduslike koosluste asendumine põllumaadega, kuid põllumajanduse pealetungist otseselt puutumata jääenud kooslusi põllumajandusmaastikus ohustavad ka ulatuslik väetiste ja pestitsiidide kasutus ning jäänuk-biotoobilaikude killustatus.

Lisaks veel säilinud metsa- ja niidulaikudele ning põldudele leidub põllumajandusmaastiku mosaiigis märkimisväärset mitmesuguseid sekundaarseid põldudega seotud kooslusi: põlluservi (näiteks teeservad, kraaviservad, metsaservad) ja väikesepinnalisi koosluselaike (kivikuhjad ja väikesed metsatukad). Nendest maaстikuelementidest koosnevate kohalike rohevõrgustike osatähtsust on elurikkuse kadumise töttu hakatud üha enam alternatiivsete kasvukohtade ja liikide võimalike „levikukoridoridena“ värtustama.

Põlluservade kitsas struktuur muudab aga sealsete taimestiku väga vastuvõtlikuks põllumajandusest lähtuva häiringu suhtes. Põldudelt leostuvad lämmastik- ja fosforvätised loovad soodsad tingimused konkurentsivõimelisemate ja kiirekasvuliste taimeliikide domineerimiseks ning põhjustavad sellega liigirikkuse vähenemist. Perioodiline herbitsiidide kasutamine soodustab lühiealiste häiringuga kohastunud elik ruderaalsete liikide osakaalu kasvu. Et peatada põllumajandusmaastike elurikkuse edasist vähenemist, on üha enam asutud erinevate Euroopa Liidu põllumajanduslike keskkonnatoetuste kaudu propageerima keskkonnasõbralike põllumajandusmeetodite kasutuselevõttu, sealhulgas ka põlluservabioopide säilitamist ja hooldamist. Samas on teadmised põlluservade rollist elurikkuse säilitamisel üpris lünklitud. Taimede puhul on näidatud, et mahepõllundus, kus herbitsiidide ja mineraalse lämmastikvätise kasutus on keelatud, avaldab otsest ja kiiret positiivset mõju umbrohtude mitmekesisusele põllul. Kuid üheselt pole õnnestunud töestada, kas ja mil määral mõjutab kõrvalasetseva põllu majandamisintensiivsus selle põllu servakoosluse taimkatet. Mitmetes uurimistöödes on küsimärgi alla seatud ka teiste põllumajanduslike keskkonnameetmete positiivne mõju põllumajandusmaastike elurikkusele.

Arvamust põlluservadest kui põllumajandusmaastike elurikkuse „pääste-rõngast“ on toetanud uurimused, kus on näidatud, et puuderibad ja hekid võivad

ökoloolgiliste tingimuste poolest pakkuda alternatiivset kasvukohta varju-nõudlikele metsaliikidele, teeservad ja teised avatud põlluservad drastiliselt kahaneenud pindalaga pool-looduslike niidukossluste iseloomulikele taimeliiki-dele ning kraaviservad niiskuslembestele liikidele. Väga harva on aga samades maastikes võrdlevalt analüüsitud eelpool mainitud põlluservatüüpide taimkatet ning detailsemalt uuritud, kas ja milliste liikide jaoks võivad põlluservad kasvukohtade kadumist komponeerida. Samuti on jäänud tähelepanuta asjaolu, missugused ökoloolgilised tingimused kujunevad mitme maastikuelemendi koosmõjul (näiteks asuvad hekid sageli just teeservades ja kraaviservades) ning kuidas see põlluserva taimekooslust mõjutab.

Et adekvaatselt hinnata põllumajandusliku maakasutuse intensiivsuse ja maastiku struktuuri mõju elurikkusele, tuleks kasutada nende tegurite suhtes tundlikke indikaatoreid. Paraku on üks enimkasutatud indikaatoreid liigirikkus. Vastupidiselt traditsioonilistele arusaamadele liigirikkusest kui kasvukoha kvaliteedi indikaatorist ei pruugi sellises ajalis-ruumiselt ebastiabilses ja häiringuterohkes keskkonnas, nagu seda on põllumajandusmaastik, liikide arv sugugi peegeldada tegelikke keskkonnatingimusi. Liikide vastus häiringutele ja maastiku struktuuri muutustele on väga varieeruv ning sõltub liigiomastest funktsionaalsetest tunnustest: näiteks leviku- ja tollemistemistüübist, kasvuvormist ja tundlikkusest inimtegevuse suhtes. Seega võiks taimkatte funktsionaalsete tunnuste mustrite analüüs anda meile oluliselt rohkem infot taimkatte kvalita-tiivisetest muutustest vastusena maakasutusele ja maastiku struktuurile. Funkt-sionaalsete tunnuste analüüs võimaldab ühtlasi prognoosida, milliseid liike maakasutuse intensiivistumine ja maastiku killustumine kõige enam ohustab, ning sestap hõlbustab ka elurikkuse kaitse planeerimist.

Kuigi funktsionaalsete tunnuste kasutamine on põllumajanduse ja maastiku struktuuri mõju hindamiseks informatiivne ja samas piisavalt üldistav lähenemisviis, vajab praktiline seiretöö vähemaa aja ja tööjõukuluga hinnatavat indikaatorit, mis oleks samas ligilähedaselt informatiivne ning tundlik ka seirata regiooni liigifondi suhtes. Nende lihtsate eelduste kätkemine ühe indikaatori alla pole aga osutunud lihtsaks ülesandeks.

Käesoleva töö peamine eesmärk oli kirjeldada põllumajandusliku maakasutuse intensiivsuse ja maastiku struktuuri mõju põllumajandusmaastike taimkatte mitmekesisusele ning funktsionaalsele ja liigilisele koosseisule (**I–IV**). Vastust otsisime ka järgmistele küsimustele: (1) kas erinevused maakasutuses ja maastiku struktuuris kajastuvad taimede funktsionaalsete tunnuste mustrites ja funktsionaalsete gruppide siseses liigirikkuses (**I**); (2) millised tunnused on kõige tundlikumad põllumajandushäiringute ja maastiku struktuuri muutuste suhtes (**I**); (3) milline on põlluservade roll põllumajandusmaastike taimestiku mitmekesisuse kaitses (**II, III, IV**); (4) millised tegurid mõjutavad põlluserva taimkatte mitmekesisust ja liigilist koosseisu (**II, III, IV**). Seadsime eesmärgiks panustada ka põllumajandusmaastike seiretemetoodikasse, katsetades taimkatte mitmekesisuse hindamisel uusi indikaatoreid (**III, IV**).

Et vastata küsimusele, kas erinevused maastiku struktuuris ja maakasutuses põhjustavad muutusi taimede funktsionaalsete tunnuste jaotumises ja mitme-

kesisuses, osalesime projektis „Greenveins”, mille raames kirjeldasime koostöös kuue Euroopa riigiga (lisaks Eestile Belgia, Prantsusmaa, Holland, Saksa-maa, Tšehhi, Šveits) 25 mäastiku taimkatte suureskaalist liigirikkust, taime-liikide funktsionaalseid tunnuseid, mäastiku struktuuri ja maakasutuse intensiivsust (**I**). Leidsime, et taimkatte funktsionaalne koosseis ja mitmekesisus on väga tundlikud sellise lihtsa mäastiku struktuuri parameetri suhtes nagu looduslike ja pool-looduslike koosluste osakaal mäastikus. Nende koosluste osakaalu vähenemise ja maakasutuse intensiivsuse kasvuga kaasnes ruderaalide, inimkaaslejate, üheaastase elutsükliga ja isetolmlevate liikide arvukuse suurenemine ning mitmeaastaste ja vegetatiivselt levivate liikide osakaalu vähenemine. Liigirikkust funktsionaalsete gruppide siseselt mõjutas samuti peamiselt looduslike ja pool-looduslike koosluste olemasolu. Sobivate kasvukohtade osakaal mäastikus oli oluline eeskätt kasvukohaspetsialistide jaoks: lõikheinalised, sõnajalgtaimed ja mitmeaastased rohundid. Kombineerides tunnuseid, mis iseloomustasid liikide invasiivsust, inimkaaslevust ning tundlikust häiringulise inimtegevuse suhtes, moodustasime uue funktsionaalse tunnuse – liikide loodusväärtslikkuse, mille kohaselt invasiivsed ja põllumajandusliku häiringu suhtes vähemtundlikud liigid said loodusväärtslikkuse skaalal madalama ning pärismaised ja häiringu suhtes tundlikud liigid kõrgema hinde. Pool-looduslike ja looduslike koosluste osakaalu suurenemine tõi kaasa kõrge loodusväärtsusega liikide mitmekesisuse kasvu, kuid madala loodusväärtsusega liigid mäastiku struktuuri muutustele ei reageerinud.

Ka maakasutuse intensiivsuse kasvuga kaasnesid märkimisväärsed muutused taimkatte mitmekesisuses. Intensiivne maakasutus põhjustas eelkõige lõikheinaliste ja sõnajalgtaimedede liigirikkuse langust mäastikus. Kui analüüsime maakasutuse mõju eraldi kõrge loodusväärtsusega ja madala loodusväärtsusega liikide liigirikkusele, ilmnes, et kõrgem maakasutuse intensiivsus soodustas madala loodusväärtsusega graminoidide mitmekesisust ning vähendas kõrge loodusväärtsusega graminoidide liigirikkust (**I**). Seega põhjustavad mäastiku killustumine, kasvukohtade kadumine ja maakasutuse intensiivstumine ulatuslikke muudatusi taimeliikide funktsionaalses koosseisus ja mitmekesisuses. Nende muutuste suhtes tundlikumad on mitmeaastased liigid, klonaalse levikuga liigid ja kasvukoha spetsialistid ning vähemtundlikud üheaastase elutsükliga sagedasi häiringuid taluvad liigid. Tulemused annavad alust prognoosida, et kasvav maakasutuse intensiivsus ja loodusmäastiku killustumine aitavad kanda kinnitada ka mittepärismaistel invasiivsetel liikidel.

Meid huvitas, mil määral põlluservad toetavad põllumajandusmäastike taimkatte mitmekesisust ning millised on põhilised tegurid, mis põlluservade taimkatet mõjutavad. Üle-euroopalise uurimuse tulemusena leidsime, et suurema põlluservade osakaaluga mäastikus kaasnes n-ö servaliikide osakaalu kasv ning kasvukohaspetsialistide mitmekesisuse langus, mis viitab sellele, et põlluservad siiski ei asenda suurepinnalisi looduslikke ja pool-looduslikke kasvukohti (**I**). Ka meie spetsiifilisemate uurimistööde tulemused (**II**, **III**, **IV**), kus analüüsime Eesti põllumajandusmäastike põlluservade taimkatte ligilist kooseisu, näitasid, et valdavalt on põlluservades kasvukoha leidnud generalistid,

mildest paljud esinevad sagedasti ka põldude umbrohuflooras. Haruldasi liike leidus põlluservades väga vähe.

Sarnaselt üle-euroopalisele uurimusele (**I**) klassifitseerisime Eestis läbiviidud uurimistöödes liigid kahte suurde rühma, võttes seekord arvesse ka regionaalsete liigifondi koosseisu (**III**, **IV**). Põldudel sagedamini esinenud liigid klassifitseerisime n-ö agrotolerantseteks liikideks ning ülejäänud liikidele, mida põldudel ei leidunud või leidus väga harva, omistasime kõrge loodusvärtusega liigi staatuse. Seejärel analüüsime maakasutuse ja maaстiku struktuuri mõju nii üldisele liigirikkusele kui ka eraldi agrotolerantsete ja loodusvärtuslike liikide liigirikkusele.

Leidsime, et põlluserva struktuur mõjutas oluliselt taimkatte liigilist koosseisu ning mitmekesisust (**II**, **III**, **IV**). Kraaviservades leidus rohkem kõrge loodusvärtusega liike, sealhulgas eeskätt niidukooslustele iseloomulikke ja niiskuslembesemaid liike. Teeserv oli sagedasem kasvukoht agrotolerantsetele liikidele, sealhulgas paljudele ruderaalsetele liikidele ja umbrohtudele. Hekkides, puuribades ja metsaservades leidus küll mõningal määral varjulembesemaid ja paiguti ka metsaliike, kuid valdavalt domineerisid siiski nitrofilised suuremakasvulised liigid, mistõttu ei saa selliste varjulismate põlluservade ökoloogilisi tingimusi pidada vörreldavaks metsa kasvukohatingimustega.

Põlluserva taimkatte mitmekesisust mõjutas ka põlluserva enda laius: loodusvärtuslikud liigid said kasu eeskätt laiemast avatud kooslusega põlluservast, kitsamas põlluservas kasvas aga rohkem agrotolerantseid liike. Seoses pool-looduslike niidukoosluste pindala vähenemisega tuleks senisest rohkem tähelepanu pöörata veel säilinud jäänuKKoosluste laikudele ja alternatiivsetele kasvukohtadele, muu hulgas ka laiadele avakooslustega põlluservadele. Meie tulemuste kohaselt peaks põlluserva laius olema vähemalt kolm kuni neli meetrit, et tagada piisavalt stabiilsed ökoloogilised tingimused ka kasvukoha-nõudlikumate niiduliikide jaoks.

Kuigi haruldusi ja kasvukohaspetsiifilisi liike leidus põlluservades suhteliselt vähe, leidsime, et madalamma maakasutuse intensiivsuse ja mahe-põllumajanduslike meetoditega ning adekvatse maaстikuplaneerimisega on siiski võimalik soodustada mitmekesisemate põlluservade püsimajäämist ja kujunemist (**III**, **IV**), ning seda eelkõige kõrgema loodusvärtusega liikide kasuks. Agrotolerantsete liikide liigirikkus erineva intensiivsusega majandatud põldude servades ei muutunud (**IV**).

Liigirikkus on olnud üks laialdasemalt kasutatud ja lihtsamaid elurikkuse seisundi indikaatoreid. Käesoleva töö tulemused viitavad aga sellele, et üksnes liikide arv pole piisav andmaks hinnangut sellise ökosüsteemi kasvukohatingimustele, nagu seda on kaasaegne häiritud põllumajandusmaastik. Liigirikkus võib olla võrdlemisi kõrge ka intensiivselt majandatava põllu servas, kuid nende liikide hulgas on tõenäoliselt suurem osakaal häiringuga kohastunud liikidel, s.o agrotolerantsetel liikidel. Nii võib üksnes liigirikkuse kasutamine varjestada elurikkuse tegeliku vastuse maakasutuse muutuste suhtes. Sestap tuleks põllumajandusliku maakasutuse intensiivuse ja maaстiku mõju hindamisel üldise liigirikkuse asemel indikaatorina kasutada nende liikide liigi-

rikkust, mis on tundlikumad põllumajandustegevuse suhtes ning mida maakasutuse intensiivistumine ja maaстиku killustumine esmajärjekorras ohustab, s.o kõrge loodusvärtusega liigid. Nende liikide sageduse kasv, kelle jaoks põllumajandustegevus pigem uusi kasvukohti loob (ehk agrotolerantsed liigid), indikeerib aga põllumajandusmaastike keskkonnatingimuste halvenemist.

Kokkuvõtteks

Leidsime, et muutused maaстиku struktuuris ja maakasutuse intensiivsusess põhjustavad ulatuslikke muudatusi taimkatte nii suure- kui väikeseskaalalisest mitmekesisuses ja funktsionaalises koosseisus. Maaстиku killustumise ja maakasutuse intensiivistumise suhtes tundlikumad on mitmeaastased ja klonaalne levikuga liigid ja kasvukohaspetsialistid ning vähemtundlikud üheaastase elutsükliga sagedasi häiringuid taluvad liigid ja generalistid. Põlluservad ei suuda täielikult asendada suurepinnaliste looduslike ja pool-looduslike koosluste olemasolu maaстиkus. Küll aga on võimalik põlluservade kasvukohatingimusi märkimisväärsest parandada, kasutades mahepõllumajandusmeetodeid ning välvides herbitsiidide ja väetiste sattumist põlluserva. Samuti tuleks põllumajanduse-keskkonnameetmete raames soodustada laiemate püsitaimestikuga põlluservade säilitamist – kitsad põlluservad pakuvad kasvukohta peamiselt ruderaalsetele ja häiringu suhtes tolerantsetele liikidele, kuid vähemalt kolme-nelja meetri laiused servad tagavad märkimisväärsest kõrgema loodusvärtuslike liikide mitmekesisuse. Soovitame põllumajandusliku maakasutuse intensiivuse ja maaстиku mõju hindamisel üldise liigirikkuse asemel indikaatorina kasutada nende liikide liigirikkust, mis on tundlikumad põllumajandustegevuse suhtes ning mida maakasutuse intensiivistumine ja kasvukohtade killustumine esmajärjekorras ohustab, s.o kõrge loodusvärtusega liigid. Nende liikide sageduse kasv, kelle jaoks põllumajandustegevus uusi kasvuvõimalusi loob (ehk n-ö agrotolerantsed liigid), viitab põllumajandusmaastike keskkonnatingimustele halvenemisele.

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- Aavik, T. 2004. Looduse ja kultuuri habras lõiming vajab hoolt. Rohtmets, I. (Ed.) Lehed ja tähed: looduse ja teaduse aastaraamat 2004: 174–175. /in Estonian/
- Aavik, T. 2003. Maastikes säilib kultuur. In: Rohtmets, I. (Ed.) Lehed ja tähed: looduse ja teaduse aastaraamat 2003: 40–44. /in Estonian/

Grants and nominations:

Personnel in grants:

- ETF7878 (Jaan Liira), The effect of dispersal limitation and anthropogenic disturbance on the development of forest vegetation in agricultural landscapes
SF0180090s08 (Martin Zobel), Vegetation patterns, species coexistence and mechanisms behind them

- 2007, 2008 Kristjan Jaak's travelling grants from SA Archimedes
2006, 2008 Research grants of the Doctoral School of Ecology and Environmental Sciences
2006, 2007 Travelling grants of the Doctoral School of Ecology and Environmental Sciences

Awarded by the Estonian Ministry for Education and Research in Estonian National Contest for Young Scientists at university level:

I prize for MSc thesis ("Vascular plant species diversity and composition in Estonian agricultural landscapes") in 2005

Diploma for BSc thesis in 2003

Winner of essay contest of the Institute of Botany and Ecology in 2001

Membership in societies:

- International Association for Vegetation Science
Estonian Naturalists' Society
Estonian Seminatural Community Conservation Association

ELULOOKIRJELDUS

I. Üldandmed

Ees- ja perekonnanimi:	Tsiipe Aavik
Sünniaeg ja -koht:	03.01.1981, Tallinn
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Praegune töökoht:	Botaanika osakond, Ökoloogia ja Maateaduste Instituut, Tartu Ülikool, doktorant
Haridus:	
2005	Tartu Ülikool, magistrikraad taimeökoloogias ja ökofüsioloogias. Magistritöö: <i>Vascular plant species diversity and composition of Estonian agricultural landscapes (Eesti põllumajandusmaastike taimkatte mitmekesisus ja liigiline koosseis)</i>
2003	Tartu Ülikool, bakalaureusekraad bioloogias.
1987–1999	Tallinna Inglise Kolledž (Tallinna 7. Keskkoool)
Keelteoskus:	
Eesti, Inglise	
Töökogemus:	
2005–2009	Botaanika osakond, Ökoloogia ja Maateaduste Instituut, Tartu Ülikool, doktorant
Alates 2002	tähtajalised töölepingud Tartu Ülikooliga: spetsialist, laborant

II. Teadustegevus

Peamised uurimisvaldkonnad:

Põllumajandusmaastike taimkatte mitmekesisus, liigiline koosseis ja funktsionaalse tunnuste mustrid. Maakasutuse intensiivuse ja maaestiku struktuuri mõju põllumajandusmaastike taimkattele. Põlluservade roll taimkatte mitmekesisuse kaitses. Põllumajanduslike keskkonnatoetuste tähtsus elurikkuse kaitses. Poollooduslike koosluste taimkatte mitmekesisust mõjutavad tegurid.

Publikatsioonide loetelu:

Artiklid, mis on kajastatud ISI Web of Science andmebaasis

- Aavik, T., Püssa, K., Roosaluste, E. & Moora, M. Vegetation change in boreonemoral forest during succession – trends in species composition, richness and differentiation diversity. *Annales Botanici Fennici* (trükis).
- Aavik, T. & Liira, J. 2009. Agrotolerant and high nature-value species – plant biodiversity indicator groups in agroecosystems. *Ecological Indicators* 9: 892–901.
- Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., Billeter, R., Bukacek, R., Burel, F., De Blust, G., De Cock, R., Dirksen, J., Edwards, P. J., Hamersky, R., Herzog, F., Klotz, S., Kühn, I., Le Coeur, D., Miklova, P., Roubalova, M., Schweiger, O., Smulders, M. J. M., van Wingerden, W. K. R. E., Bugter, R. & Zobel, M. 2008. Plant functional group composition and large-scale species richness in the agricultural landscapes of Europe. *Journal of Vegetation Science* 19: 3–14.
- Aavik, T., Augenstein, I., Bailey, D., Herzog, F., Zobel, M. & Liira, J. 2008. What is the role of local landscape structure in the vegetation composition of field boundaries? *Applied Vegetation Science* 11: 375–386.
- Aavik, T., Jõgar, Ü., Liira, J., Tulva, I. & Zobel, M. 2008. Plant diversity in a calcareous wooded meadow – The significance of management continuity. *Journal of Vegetation Science* 19: 475–484.

Artiklid teistes rahvusvahelistes ajakirjades

- Liira, J., Aavik, T., Parrest, O. & Zobel, M. 2008. Agricultural sector, rural environment and biodiversity in the central and eastern European EU member states. *Acta Geographica Debrecina Landscape and Environment Series* 2: 46–64.

Populaarteaduslikud artiklid

- Aavik, T. 2004. Liigirikkus – tasakaalu või tasakaalutuse tulemus? *Tulva*, I., Öpik, M. & Puura, I. (Toim.) *Tasakaalu teoria – Schola Biotheoretica* 30: 63–69.
- Aavik, T. 2004. Looduse ja kultuuri habras lõiming vajab hoolt. *Rohtmets*, I. (Toim.) *Lehed ja tähed: looduse ja teaduse aastaraamat* 2004: 174–175.
- Aavik, T. 2003. Maastikes säilub kultuur. *Rohtmets*, I. (Toim.) *Lehed ja tähed: looduse ja teaduse aastaraamat* 2003: 40–44.

Konverentside ettekanded:

- Aavik, T. & Liira, J. 2008. The vegetation of agroecosystems – the role of land use and landscape structure. In: EURECO-GFOE 2008. Proceedings: EURECO-GFOE 2008. Biodiversity in an Ecosystem Context; Leipzig; 15–19. Sep 2008. (Toim.) Stadler, J., Schöppe, F. & Frenzel, M., 2008, 737 – 737.
- Aavik, T., Jõgar, Ü., Liira, J., Tulva, I.; Zobel, M. 2008. Plant species composition and diversity in a calcareous wooded meadow – the significance of

- management continuity. In: 6th European Conference on Ecological Restoration. Abstract Book: 6th European Conference on Ecological Restoration. Towards a sustainable future for European ecosystems; Ghent, Belgia; 8–12. Sep 2008, 153–153.
- Aavik, T., Zobel, M. & Liira, J. 2007. The effects of landscape structure on the vegetation of field boundaries in Estonia. In: Proceedings of the 7th IALE World Congress: International Association of Landscape Ecology 2007. 25 Years of Landscape Ecology: Scientific Principles in Practise; Wageningen, Holland; 8–12 July 2007. (Toim.) Bunce, R.G.H., Jongman, R.H.G., Hojas, L. & Weel, S. 2007, 1117.
- Aavik, T., Zobel, M. & Liira, J. 2007. The influence of landscape structure on the field margin vegetation of Estonian agricultural landscapes. In: New Zealand: New home; new habitat! new ideas? Book of Abstracts: 49th Annual Conference of the IAVS – New Zealand; 12–16 February 2007. (Toim.) van Essen, R. A., 95.
- Aavik, T. & Liira, J. 2006. The distribution of plant functional types in Estonian agricultural landscapes. In: 8th clonal plant workshop: 8th clonal plant workshop – generality, specificity and diversity of clonal growth; Pärnu, Estonia; June 27–30, 2006. (Toim.) Sammul, M., Kull, T., Kull, K. & Tali, K., 2006, 47.

Uurimistoetused ja stipendiumid:

Osalus grantides:

- ETF7878 (Jaan Liira), Metsakoosluste kujunemist mõjutavad ökoloogilised ja antropogeensed tegurid põllumajandusmaastikus
 SF0180090s08 (Martin Zobel), Taimkattemustrid, liikide kooseksisteerimine ja seda põhjustavad mehhanismid

2007, 2008 Kristjan Jaagu välislähetuse stipendum

2006, 2008 Ökoloogia ja Keskkonnateaduste doktorikooli stipendum teadustöö
 2006, 2007 Ökoloogia ja Keskkonnateaduste doktorikooli välislähetuse stipendum

Eesti Teadus- ja Haridusministeeriumi üliõpilaste teadustööde riiklik konkurss:
 I preemia magistriõpppe astmes magistritöö *"Vascular plant species diversity and composition in the Estonian agricultural landscapes"* eest aastal 2005

Diplom bakalaureusetöö "Vihtra ja Viiratsi põllumajandusmaastike taimkatte iseloomustus ja seda mõjutavad tegurid" eest aastal 2003

I auhind botaanika ja ökoloogia instituudi esseekonkursil 2001

Liikmelisus erialastes organisatsioonides:

Rahvusvaheline Taimkatteteaduse Assotsiatsioon

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