

## Meetings

### New insights into vegetation patterns and processes

#### 56th Annual Symposium of the International Association for Vegetation Science, in Tartu, Estonia, June 2013

A basic question in vegetation science is – what ecological and evolutionary processes create the patterns that we observe (Fig. 1)? Considerable descriptive information about vegetation structure is available for many regions of the world. Major forces linked to particular vegetation patterns are also known: evolution (availability of regional species pools), dispersal (how organisms reach a location), abiotic (climatic, soil conditions) and biotic (competition, facilitation, parasitism, mutualism) factors. However, the question of how these mechanisms interact to shape vegetation patterns remains largely open. This question becomes increasingly relevant as novel ecosystems emerge, native species change their ranges and alien species arrive, establish and become dominant, having profound impacts on a range of ecosystem functions and ecosystem services.

This is the context in which the 56th Annual Symposium of the International Association for Vegetation Science (IAVS), ‘Vegetation patterns and their underlying processes’, was held at the University of Tartu, Estonia, on 26–30 June 2013 (Fig. 2). The meeting attracted over 450 participants from 41 countries.

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*‘... the accessibility of molecular plant and plant-related microbial identification methodologies in underground samples is predicted to dramatically increase the related publication numbers in the near future ...’*

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#### Productivity–diversity relationships

Patterns and distributions of plant diversity across landscapes have been well documented for decades, but understanding why such patterns exist continues to challenge scientists (Adler *et al.*, 2011; Fridley *et al.*, 2012). One of the more common factors thought to control the number of plant species in an area is the net primary

productivity, and yet it is also among the most hotly debated topics in ecology, as many researchers see productivity as an outcome of species diversity itself.

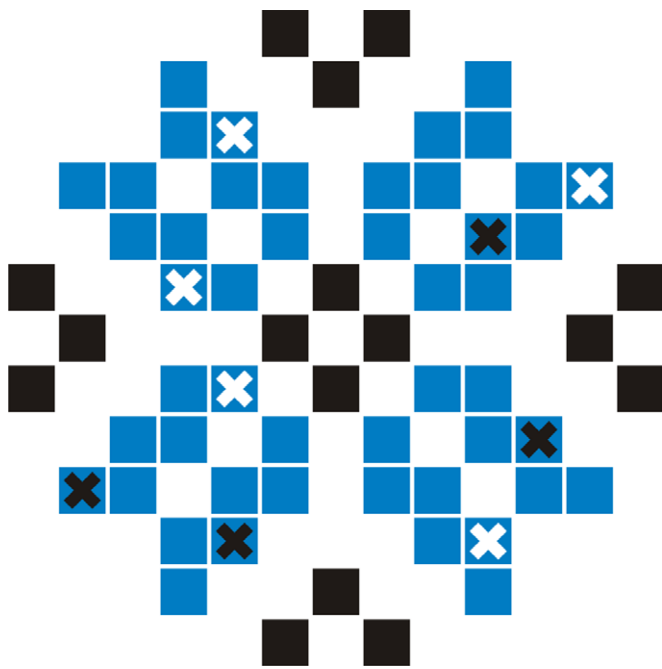
Philip Grime’s hump-backed model (HBM) predicts a unimodal relationship between herbaceous plant species richness and aboveground biomass, such that maximum species richness is found at intermediate biomass (as a proxy of productivity), and minimum species richness is found at low and high biomass (Grime, 1973a,b, 1977). Lauchlan Fraser (Thompson Rivers University, Kamloops, BC, Canada) highlighted the importance of a global coordinated distributed experiment (CDE) (Fraser *et al.*, 2013) to test the HBM in herbaceous plant communities at multiple scales. He emphasized the need to ensure that litter was included in the measurement of aboveground biomass as a proxy to productivity, and that there was adequate representation of sites from a wide range of productivities.

In addition to plant biomass, spatial heterogeneity within and between sites may help to explain diversity patterns in grasslands along productivity gradients. Carl Beierkuhnlein (University of Bayreuth, Germany) and Riin Tamme (University of Tartu, Estonia) showed examples of how the assessment of beta diversity patterns and heterogeneity in productivity within and across sites helps to elucidate the productivity–diversity relationship. A growing body of work focusing on plant traits has revealed that patterns in ecosystem function are linked to functional rather than taxonomic diversity. For example, Anke Jentsch (University of Bayreuth, Germany) showed that the plant foraging value had unimodal, and plant height and specific leaf area linear positive, relationships with productivity. Lucas Enrico (IMBIV (CONICET-UNC), Cordoba, Argentina) further illustrated ways to include plant functional trait diversity in a community for the analysis of HBM-related questions.

The HBM expresses the maximum potential species richness by total biomass. Therefore, within the HBM, there is typically large variation in species richness by total aboveground biomass, especially at the intermediate range of aboveground biomass. Drivers that can account for variation in species richness may be attributed to a number of abiotic and biotic factors, as well as historical factors. Sandor Bartha (MTA Centre for Ecological Research, Vácrátót, Hungary) and Camilla Wellstein (University of Bayreuth, Germany) explored the relative importance of dominant plants and their correlation with species and functional diversity. David Ensing (University of British Columbia, Kelowna, BC, Canada) illustrated how cattle grazing influenced beta diversity positively at a low productivity site, but negatively at a high productivity site, suggesting that productivity modulates the effect of herbivory on plant diversity. The increasing field of plant-related microbial research was exemplified by Jonathan Bennett (University of Alberta, Edmonton, AB, Canada), who found that arbuscular mycorrhizal (AM) fungi increased plant diversity, but



Fig. 1 Vegetation pattern in a raised bog at Männikjärve, Endla Nature Reserve, Estonia. Photograph courtesy of Edgar Karofeld.



## IAVS 2013 TARTU

Fig. 2 Logo of the 56th Annual Symposium of the International Association for Vegetation Science (IAVS), 'Vegetation patterns and their underlying processes', held at the University of Tartu, Estonia, on 26–30 June 2013. Courtesy of Rein Kalamees.

only when fertilizer was added and litter removed. This indicates that resource stoichiometry, rather than absolute resource quantities, best explain AM fungal effects on plant diversity. Historical factors influence available species pools, initial community states and community assembly trajectories, illustrated by Maria Höhn (Corvinus University of Budapest, Hungary). For example, seed addition, a species pool amendment, can support species richness a full 6 yr after treatment, even when fertilized, as shown by Bryan Foster (University of Kansas, Lawrence, KS, USA).

Patterns to support the HBM exist, but evidence suggests that many different processes seem to drive these patterns, perhaps simultaneously.

## Community assembly

Plant diversity patterns can be examined using functional traits to infer the relative importance of abiotic and biotic processes governing assembly among communities, and along environmental gradients. Many studies addressed this, and take-home messages from the meeting highlighted that methodological issues need to be carefully considered, as well as above- and belowground processes, different spatial and temporal scales, and trophic levels.

Commonly, processes driving community assembly are inferred by exploring functional, phylogenetic or species (taxonomic) diversity patterns. The observed patterns are compared with that expected by chance (a null model) using randomization tests (Götzenberger *et al.*, 2012). Functional trait convergence and phylogenetic clustering, whereby species are more similar, or closely related, than expected by chance, is attributed to processes that tend to increase similarity among co-occurring species – often habitat filtering or competition. The opposite, trait divergence or phylogenetic overdispersion, whereby species are more dissimilar, or distantly related, than expected by chance, is usually attributed to limiting similarity or environmental heterogeneity (Weiher & Keddy, 1995; de Bello *et al.*, 2012).

Null models generate patterns that would emerge randomly. Lars Götzenberger (Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic) discussed the important implications and ecological assumptions incorporated into different null models. Importantly, the answer obtained largely depends on the type of null model employed. Of similar importance is the choice of the dissimilarity measures and functional diversity indices (Mouchet *et al.*, 2010; de Bello *et al.*, 2013), and how the species pool is defined. Several studies highlighted the relevance of the effects of environmental gradients, and intraspecific trait variation. For example, Zoltán Botta-Dukát (MTA Centre for Ecological Research, Vácrátót, Hungary) found trait convergence among species from heterogeneous environments, and trait divergence among species from homogeneous environments, as suggested by de Bello *et al.* (2012).

Grasslands are useful model systems to study community assembly patterns. This was apparent at the meeting, and is illustrated here by the following three studies conducted in Estonian grasslands. Jodi Price (University of Western Australia, Crawley, WA, Australia) investigated 33 grasslands and demonstrated convergence of most functional traits at very small scales. This was most probably a result of micro-environmental filtering, whereby small-scale environmental heterogeneity increased the functional diversity in the species pool. Liina Saar (University of Tartu, Estonia) examined trait assembly across a gradient of land use, and found that community assembly was dependent on community stability. Namely, small-scale trait divergence was detected in stable grasslands, possibly as a result of limiting similarity, whereas convergence was found in dynamic, overgrown sites and road verges. Antonio Gazol (University of Tartu, Estonia)

found that juniper encroachment reduced plant species richness and functional diversity, with both species richness and functional diversity increasing with distance from the juniper canopy. These studies highlight that multiple processes drive community assembly, even within similar communities, depending on land use, woody plant cover and disturbance.

Recent studies have highlighted the importance of belowground processes in community assembly. Pille Gerhold (University of Tartu, Estonia) found evidence for different assembly processes in above- and belowground portions of the plant community (cf. Price *et al.*, 2012). Tomáš Herben (Institute of Botany, Czech Academy of Sciences, Pruhonice, Czech Republic) also demonstrated that neglecting belowground traits, mostly plant clonal growth strategies, can overlook important patterns in community assembly.

Few studies have examined assembly processes along temporal scales, but it is becoming apparent that patterns and processes can differ dramatically in different years with varying climatic conditions. Carlos P. Carmona (Universidad Autonoma de Madrid, Spain) demonstrated that temporal resource fluctuations affected community assembly, with a shift in traits indicative of size-symmetric competition for belowground resources in dry years, to size-asymmetric competition for light in wet years. Over much longer time scales, along a successional gradient, Mark Leithead (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) reported opposite patterns in structural traits in temperate and tropical forests, as well as some commonalities.

Multi-trophic community assembly work is an area of increasing interest (for a recent publication on this topic, see Moretti *et al.*, 2013), and will have important theoretical and applied implications. Robin Pakeman (The James Hutton Institute, Aberdeen, UK) illustrated this by showing that plant response traits successfully explained the distribution of carabid beetle functional traits across various habitats.

## Species pool and the dark side of diversity

Ecological theory and biodiversity conservation have traditionally relied on the diversity of the species observed. However, this observed diversity represents only a portion of the actual 'species pool', that is all the species in a region that can potentially inhabit those ecological conditions. The species absent from an ecosystem, but belonging to its species pool, constitute the 'dark diversity' of a site (Pärtel *et al.*, 2011).

Several studies and discussions during the meeting showed that a knowledge of the species pool and dark diversity of a site allows a more thorough evaluation of the roles of local and regional processes in ecological communities, including their restoration potential, and the conservation values of given sites and regions. The plenary talk by Meelis Pärtel (University of Tartu, Estonia) was an exciting attempt to clarify the concepts, terminology and different components of dark diversity, particularly highlighting the distinction between species truly absent from the community and those apparently absent, but actually being dormant below ground. Milan Chytrý (Masaryk University, Brno, Czech Republic) employed the species pool concept

to explain the high diversity grasslands in the Czech Republic. Petr Pyšek (Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic) further showed how the size of the species pool, with its dark diversity, is fundamental in determining plant invasion patterns. Finally, Ove Eriksson (Stockholm University, Sweden) showed connections between the evolutionary formation of species pools in a human-made landscape and present conservation and management practices (Eriksson, 2013).

Although the species pool size and composition are often important predictors of local biodiversity patterns, several presented studies further demonstrated the importance of the diversity of functional traits within species pools – that is, the 'functional species pool' (de Bello *et al.*, 2012). Sebastian Schmidlein (Karlsruhe Institute of Technology, Germany) showed how to use the trait composition of species pools to build models that are able to generate maps of plant communities across complex landscapes featuring strong temporal dynamics. Similarly, Corina Basnou (CREAF, Cerdanyola del Valles, Spain) and Jakub Tesitel (University of South Bohemia, České Budějovice, Czech Republic) used species pools and traits to assess species distribution models in complex landscapes.

The concept of the species pool and, similarly, the recent concept of dark diversity have long fascinated ecologists, but have also generated a certain perplexity. Although recognizing the great potential of the concepts, doubts have been raised about the possibilities to actually estimate the absent species of a site, which, by definition, cannot be observed and therefore measured. Recent advances in ecoinformatics, however, have increased the possibilities of determining environmentally and geographically delimited species pools on the basis of large databases. Francesco de Bello (Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic) compared results of species pool estimates obtained with several methods and demonstrated a good degree of concordance between expert-based and computational approaches. Bryndís Marteinsdóttir (Stockholm University, Sweden) demonstrated that species added by sowing and transplanting establish better if they belong to the dark diversity component of the local species pool than species not expected in the species pool. Modern DNA-based techniques can further help to define which species are apparently absent in the observed diversity, but may be hidden below ground, and could potentially occur in a community. These studies demonstrate the utility of the species pool and dark diversity concepts, still seen by many as impractical.

## Under the ground

Plant ecology at large and vegetation science in particular have mostly been aboveground disciplines. However, as presented above, many other important processes rather than just plant nutrient and water uptake, which determine vegetation patterns, occur under the ground. Traditionally, anything under the soil surface was seen as uniform abiotic plant growth substrate. Inspiring insight was provided by Hans de Kroon (Radboud University Nijmegen, the Netherlands) into the processes taking place under the ground – plant (root) growth patterns, plant–plant

competition and interactions with microbes – and how these play a role in shaping vegetation patterns.

Many ecosystems of the world harbour the majority of their biomass below ground in the form of plant roots (Pärtel *et al.*, 2012). Scott Wilson (University of Regina, SK, Canada) demonstrated that the majority of litter production can also occur below ground. The team of Meelis Pärtel further showed that plant communities are more species rich below ground than above ground at small and intermediate scales (Hiiesalu *et al.*, 2012). Furthermore, Inga Hiiesalu (University of Tartu, Estonia) found that plant belowground richness and biomass are related to the diversity of root symbiotic AM fungi. This is the first time that this relationship has been investigated in a natural ecosystem, having been made possible by the application of molecular methods for the identification of both partners of the symbiosis. The fast-developing fields of molecular plant (root) (Pärtel *et al.*, 2012) and AM fungal detection and identification (Gorzalak *et al.*, 2012; Öpik *et al.*, 2013) have now met, and are promising to shed more light on the co-occurrence patterns of these organisms. Covariation of AM fungal and plant diversity was further addressed by Martin Zobel (University of Tartu, Estonia), who proposed that plants ‘farm’ their symbiotic mycorrhizal fungal assemblage, reshaping it according to their own needs. This would lead to changes in local plant abundances, and would affect plant–plant interactions, and interactions with other organisms. Indeed, Mari Moora (University of Tartu, Estonia) highlighted how mycorrhizal status as a plant trait (Hempel *et al.*, 2013) could be used to better understand vegetation patterns.

Knowledge of how plant-associated microbes shape vegetation patterns is directly applicable for vegetation restoration. Adeline Bulot (Université d’Avignon, France) and Jasper Wubs (NIOO, Wageningen, the Netherlands) addressed the use of soil transplantation as part of the process of restoration of specific steppe vegetation at Le Crau, southern France and temperate grassland in Holland, respectively. Earlier research has shown that late successional plants benefit from whole-soil inoculation with soil from late-successional grassland (Kardol *et al.*, 2006). More targeted research in this field is ongoing in many laboratories and will shed more light on this topic soon.

A little studied area, because of its complexity, is the impact of AM fungi on host plant reproductive success. Sandra Varga (University of Jyväskylä, Finland) introduced the field with an example of intra- and interspecific competition of a plant species with separate sexes, *Antennaria dioica*. The more complex effects, reaching across generations, are less understood. A recent review on sex-specific positive and negative biotic interactions of dioecious and gynodioecious plants, including mycorrhiza, herbivory, pollination and pathogen–parasite interactions, provides an overview of the topic (Vega-Frutos *et al.*, 2013), which is prone to gain increasing interest from both the basic and applied sciences.

As suggested by Hans de Kroon, the coming years will bring a deeper understanding of how soil microbiota determines plant coexistence. In particular, the accessibility of molecular plant and plant-related microbial identification methodologies in underground samples is predicted to dramatically increase the

related publication numbers in the near future, and change our understanding of both above- and belowground vegetation processes.

## Future directions

Vegetation science is at a time at which the boundaries between plant science, genetics, microbiology and other related research fields are disappearing. The increased understanding, methodologies, collaborations and software developments, and novel hypotheses raised by vegetation scientists about plant community assembly, functional diversity, productivity–diversity relations, dark diversity and so on, are equally applicable beyond the strict boundaries of the discipline. Vegetation scientists themselves are digging more and more below ground, studying plant-associated (micro-)organisms and using novel molecular methods that make it possible to obtain answers to questions previously unreachable. The processes behind the patterns are becoming ever more clearly revealed.

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## References

Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Herpole WS, O’Halloran LR, Grace JB, Anderson TM *et al.* 2011. Productivity is a poor predictor of plant species richness. *Science* **333**: 1750–1753.

- de Bello F, Carmona CP, Mason NWH, Sebastia M, Lepš J. 2013. Which trait dissimilarity for functional diversity: trait means or trait overlap? *Journal of Vegetation Science* 24: 807–819.
- de Bello F, Price JN, Münkemüller T, Liira J, Zobel M, Thuiller W, Gerhold P, Götzenberger L, Lavergne S, Lepš J *et al.* 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93: 2263–2273.
- Eriksson O. 2013. Species pools in cultural landscapes – niche construction, ecological opportunity and niche shifts. *Ecography* 36: 403–413.
- Fraser LH, Henry HAL, Carlyle CN, White SR, Beierkuhnlein C, Cahill JF, Casper BB, Cleland E, Collins SL, Dukes JS *et al.* 2013. Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment* 11: 147–155.
- Fridley JD, Grime JP, Huston MA, Pierce S, Smart SM, Thompson K, Börger L, Brooker RW, Cerabolini BEL, Gross N *et al.* 2012. Comment on “Productivity is a poor predictor of plant species richness”. *Science* 335: 1441.
- Gorzelak MA, Holland TC, Xing X, Hart MM. 2012. Molecular approaches for AM fungal community ecology: a primer. *Journal of Microbiological Methods* 90: 108–114.
- Götzenberger L, de Bello F, Bräthen KA, Davison J, Dubuis A, Guisan A, Lepš J, Lindborg R, Moora M, Pärtel M *et al.* 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews* 87: 111–127.
- Grime JP. 1973a. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1: 151–167.
- Grime JP. 1973b. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Hempel S, Götzenberger L, Kühn I, Michalski SG, Rillig MC, Zobel M, Moora M. 2013. Mycorrhizas in the Central European flora – relationships with plant life history traits and ecology. *Ecology* 94: 1389–1399.
- Hiiesalu I, Öpik M, Metsis M, Davison J, Vasar M, Moora M, Zobel M, Wilson SD, Pärtel M. 2012. Plant species richness belowground: higher richness and new patterns revealed by next generation sequencing. *Molecular Ecology* 21: 2004–2016.
- Kardol P, Bezemer TM, van der Putten WH. 2006. Temporal variation in plant–soil feedback controls succession. *Ecology Letters* 9: 1080–1088.
- Moretti M, de Bello F, Ibanez S, Fontana S, Pezzatti GB, Dziock F, Rixen C, Lavorel S. 2013. Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. *Journal of Vegetation Science* 24: 949–962.
- Mouchet MA, Villegger S, Mason NWH, Mouillet D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24: 867–876.
- Öpik M, Davison J, Moora M, Zobel M. 2013. DNA-based detection and identification of Glomeromycota: the virtual taxonomy of environmental sequences. *Botany*. doi: 10.1139/cjb-2013-0110.
- Pärtel M, Hiiesalu I, Öpik M, Wilson SD. 2012. Below-ground plant species richness: new insights from DNA-based methods. *Functional Ecology* 26: 775–782.
- Pärtel M, Szava-Kovats R, Zobel M. 2011. Dark diversity: shedding light on absent species. *Trends in Ecology and Evolution* 26: 124–128.
- Price JN, Hiiesalu I, Gerhold P, Pärtel M. 2012. Small-scale grassland assembly patterns differ above and below the soil surface. *Ecology* 96: 1290–1296.
- Vega-Frutis R, Mungia-Rosas MA, Varga S, Kytöviita MM. 2013. Sex-specific patterns of antagonistic and mutualistic biotic interactions in dioecious and gynodioecious plants. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 45–55.
- Weiber E, Keddy PA. 1995. The assembly of experimental wetland plant communities. *Oikos* 73: 323–335.

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