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Macroecology of vegetation – lessons learnt from the Virtual Special Issue

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Macroecology

Macroecology uses statistical tools and broad-scale data to understand general ecological principles. It has established itself as a solid research field over the past three decades (McGill 2019). A central tenet is that emergent properties of large ecological systems can be tackled when analyzed as a whole, leaving aside much of contingency (Lawton 1999). Macroecological principles have been used for centuries, but James Brown and Brian Maurer coined the term in

their seminal paper in 1989 (Brown & Maurer 1989). Initially restricted to body size, population density, and geographical ranges, macroecology soon expanded to cover many more fields at the interface between ecology, geography, and conservation science (Blackburn & Gaston 1998). Modern macroecology is a very active discipline as indicated by a five- to six-fold increase in the number of scientific publications with the keyword “macroecology” during the past two decades, corresponding to twice the rate of increase in ecological papers in general (keyword “ecology”; source: webofknowledge.com, accessed Dec 2021).

Why macroecology of vegetation?

Macroecological approaches are also increasingly used in vegetation science (Chytrý et al. 2019). Vegetation science has a long history in broad-scale approaches that range from mapping vegetation types and vegetation properties to using plant geographical data to calculate regional properties of plant assemblages (van der Maarel & Franklin 2013). While these works have provided valuable general descriptions of vegetation, a macroecological approach might help move towards more inferential large-scale science, understand the underlying processes behind the distribution of plant communities, and disentangle the relative impacts of different factors across space and time. In short, the macroecology of vegetation might lead towards a more predictive vegetation science, which is compelling in a rapidly changing world.

Macroecology of vegetation is fuelled by recent advances in ecoinformatics, especially the compilation of large vegetation-plot databases. With such data, we can better understand how evolutionary history and varying abiotic and biotic conditions influence local plant communities across different regions and spatial scales. When analyzed together, carefully collected descriptions of local plant communities have an emergent added value.

Journal of Vegetation Science recognizes the importance of broad-scale data-driven approaches that seek mechanistic explanations. It states in its scope that the journal *publishes papers on all aspects of plant community ecology and macroecology of vegetation*. Thus, there is a journal that specifically welcomes studies on the macroecology of vegetation.

The macroecological focus of the journal has now been highlighted by a Virtual Special Issue entitled “Macroecology of vegetation”, organized by the authors of this Editorial. In March 2020, we announced the plan on social media and contacted several potential authors. The call received a warm response, and soon we had over 50 proposals of contributions. After carefully screening the preliminary abstracts, we invited 33 of them to submit the full paper, 20 of which were finally accepted for publication. Since the *Journal of Vegetation Science* moved to the continuous online-only publishing model in 2021, all papers appeared in their final form shortly after acceptance, but a Virtual Special Issue of all papers is online:

<https://onlinelibrary.wiley.com/page/journal/16541103/homepage/VirtualIssuesPage.html> .

Contributions in the Special Issue

In the following, we briefly introduce the 20 contributions included in the Virtual Special Issue, arranged by overarching topics and elaborating their foci and achievements.

Macroecology of local plant assemblages (vegetation plots)

A decade ago, Beck et al. (2012) identified the lack of small-grain large-extent data as a major deficit in macroecology. For plants, this Special Issue demonstrates that many studies and large initiatives have addressed this gap since then. A total of 15 contributions used fine-grain plant community data to address macroecological questions at various extents: global (Kusumoto et al. 2021; Testolin et al. 2021), across the whole Palaearctic (Biurrun et al. 2021; Dembicz et al. 2021; Zhang et al. 2021), across Europe (Axmanová et al. 2021; Boonman et al. 2021; Padullés Cubino et al. 2021; Sporbert et al. 2021; Večera et al. 2021), larger parts of Europe (Cao Pinna et al. 2021; Wagner et al. 2021) or at state level (Bourgeois et al. 2021; Craven et al. 2021). Most of these studies rely on two large vegetation-plot databases established and maintained by two working groups of IAVS, the European Vegetation Archive (EVA; Chytrý et al. 2016) by the European Vegetation Survey (Axmanová et al. 2021; Boonman et al. 2021; Padullés Cubino et al. 2021; Cao Pinna et al. 2021; Sporbert et al. 2021; Večera et al. 2021; Wagner et al. 2021) and the GrassPlot database (Dengler et al. 2018) by the Eurasian Dry Grassland Group (Biurrun et al. 2021; Dembicz et al. 2021; Zhang et al. 2021). Testolin et al. (2021) used data from the global vegetation-plot database sPlot (Bruehlheide et al. 2019), and four relied on regional data compilations (Bourgeois et al. 2021; Craven et al. 2021; Kusumoto et al. 2021; Tordoni et al. 2021). This pattern highlights that community efforts of collating extensive collaborative vegetation-plot databases, such as EVA, sPlot and GrassPlot, have the potential to facilitate new research avenues (Dengler et al. 2011; Wiser 2016; Bruehlheide et al. 2019), often beyond the initial scopes imagined by the founders of these databases, not mentioning the aims of most original field workers.

The 14 plot-based macroecological studies cover a highly diverse array of topics, but one pattern recurs. The fractions of explained variance in statistical models were generally much lower than 'usual' in coarse-grain macroecological studies, where often two or three predictors are enough to reach an R^2 of more than 50%. For example, Dembicz et al. (2021) found a mean R^2 for single predictors of fine-grain beta diversity of vascular plants of 7%, and Wagner et al. (2021) could only explain 21% of the variation in alien species covers, even with a multiple regression with 13 predictors. These results are in line with other fine-grained studies at large extents (e.g., Bruehlheide et al. 2018). Even if models with relatively low R^2 were well interpretable, there is evidently a need for further research on patterns, processes and suitable methods on fine-grain / large-extent vegetation studies.

Composition of floras across large geographic extents

Plant assemblages can be studied at any spatial grain, including much larger areas than classical vegetation plots (Palmer & White, 1994). This Virtual Special Issue also features some papers that investigate large extent, coarse grain patterns. Andrew et al. (2021) modelled floristic composition of 100-km² grid cells to analyze patterns of functional diversity in the vascular plants of Australia. A remarkable finding of this study was that functional diversity was strongly and non-linearly related to species richness, without any apparent saturation. Cupertino-Eisenlohr et al. (2021) used species presences of nearly 2,000 circular areas of 78 km² in the Neotropics to analyze factors differentiating their species composition. The authors found that local environmental factors, such as soil pH and topographic wetness index, were far

more important than macroclimate and dispersal barriers. This information is vital for conservation planning – protection principles cannot be generalized too widely since there is a variation in how the environment is related to plant assemblages across the Neotropics.

Functional traits and functional diversity

Functional traits and functional diversity are emerging topics in the macroecology of vegetation. Combining 740,000 vegetation plots and a large chorological database of Europe, Sporbert et al. (2021) investigated which functional traits best explain different dimensions of species performance: mean local cover, geographic range size, and climatic niche width. All three dimensions of species performance most strongly increased with specific leaf area (SLA), while other traits varied between the dimensions. From the three dimensions, the mean local cover was best explained by SLA and leaf area, including also their interaction. The authors suggested that large, acquisitive leaves are the “best” ecological strategy to achieve high cover in local plant communities. For native woody species of Hawaii, Craven et al. (2021) similarly found a positive relationship between being locally abundant and being widespread, but functional traits describing dispersal capacity or competitive ability had a minor effect on either abundance or occupancy.

Two studies related community-weighted means (CWMs) of plant functional traits to environmental drivers. Using more than 5,000 alpine vegetation plots worldwide, Testolin et al. (2021) found that their coarse-scale variables accounted for only 16.6% of the functional dissimilarity among plots, meaning that more than four-fifths of the variation is due to other drivers or is caused by noisy data. The authors found indications that the evolutionary history of alpine plant communities might be more relevant for trait composition than environmental filtering by climate, since the biogeographic realm explained a bigger proportion of the variation than the two climate-related factors in their models (vegetation zone and climatic group). Bourgeois et al. (2021) provide an example of how anthropogenic processes can decouple natural trait-environment relationships. By relating CWMs of three leaf traits to growing season length in agricultural systems, they tested for differences between grasslands and croplands. Mean functional traits of grassland communities responded more strongly to climate than those of arable communities, meaning that the intensive management of arable fields largely overrides the climatic imprint. In both cases, however, the direction of the relationship was similar: at longer growing seasons, plant communities are disproportionately composed of species with more acquisitive strategies.

Two studies explored how taxonomic and functional diversity are related across large biogeographic gradients. Both found overall high similarity in spatial patterns of the two facets of biodiversity but also noticeable deviations. Studying plot-scale patterns of grassland vegetation in Europe, Boonman et al. (2021) found pronounced trait divergence at extremely low minimum temperatures and low precipitation combined with high seasonal precipitation variability (i.e. typical Mediterranean climate). At much coarser grain of regional floras, Andrew et al. (2021) found deviations from the generally strong positive relationship of the two biodiversity facets in parts of SW Australia with a Mediterranean climate, where functional diversity was much lower than expected from the high species richness. This points to a strong trait convergence among the species in this region. It will be a task for future studies to identify the processes that

generate the deviations from the rule – in particular because Mediterranean-climate regions showed opposite deviations on the two continents.

A study from Greenland explored how shrubs with different traits respond to climate, topography, and biotic variables (Von Oppen et al. 2021). The abundance of different functional groups varied much in their responses, and there were complex interactions between abiotic and biotic factors. These results might improve our predictions on the possible future vegetation changes in the Arctic, but more data and studies on the factors modulating climate responses are needed.

Beta diversity, species-area relationships and other scaling laws

Padullés Cubino et al. (2021) studied the turnover component of between-plot beta diversity in beech forests of Europe, considering both taxonomic and phylogenetic diversity. These metrics of turnover were highly correlated and generally highest at the distribution margins of beech forests – which is not surprising given the higher average distance of the focal grid cell to all other grid cells. However, the higher phylogenetic turnover at the margins of the beech distribution remained even after controlling for species turnover, indicating that species typical of other forest types might be present there. Kusumoto et al. (2021) had a similar approach to analyze the beta diversity of angiosperm tree communities across the globe. They compared taxonomic diversity at four taxonomic resolutions (species, genus, family, order). The distance decay of similarity, logically, decreased with increasing taxonomic rank. Highlighting the non-stationarity of processes determining species composition across regions of the world, the authors found marked differences in distance decay curves between the seven distinguished regions on the globe, with the strongest distance decay at the species level in South America and the weakest in Western Eurasia. However, the pattern became more and more blurred towards higher taxonomic ranks.

Fine-grain beta diversity was the topic of three studies based on the GrassPlot database. Based on the previous finding that the power function is generally the best approximation of the species-area relationship (SAR) even at very fine grains (10^{-4} - 10^3 m²; Dengler et al. 2020); two studies used the modelled exponent of the power function (z-value) as a measure of multiplicative beta diversity within nested-plot series (Dembicz et al. 2021, Zhang et al. 2021). Dembicz et al. (2021) found consistent differences in z-values between three studied taxonomic groups in relation to elevation and to land-use intensity and used their findings to propose a new conceptual model for separating causes of fine-grain beta diversity. Zhang et al. (2021) went a step further and asked whether the small deviations from the power-law show any regularities. They dissected the SAR into segments between two subsequent grain sizes to test for potential scale-dependences between the respective “local” z-values and found that the result depends on the way vegetation was sampled in the field. If z-values vary between plant community types (Dembicz et al. 2021), then logically, SARs must intersect, and the “ranking” of community types by alpha diversity will change across grain sizes. This phenomenon could be demonstrated by Biurrun et al. (2021), who visualized the alpha diversity hotspots and coldspots in Palaearctic open vegetation types across seven grain sizes. While some regions are very diverse at any of these grain sizes and others at none, there are also regions that are species-rich at the finest

grain but species-poor at larger grain (e.g. the hemiboreal zone in Europe), or poor at a fine grain, but rich at larger grain (e.g. some regions of the Mediterranean Basin).

Alien species and plant invasions

Two studies compared the ecology of native and alien species. Tordoni et al. (2021) used vegetation plots of coastal dune habitats worldwide to derive models explaining the species richness of native and alien species. For native species, abiotic variables were more important, while for alien species, anthropogenic variables prevailed, as they were largely correlated to the gross domestic product (GDP) of the respective country. Comparing native and alien woody species of Hawaii, Craven et al. (2021) found that aliens did not show a strong positive relationship between relative abundance and relative occupancy, as did the natives. However, at a closer look, it turned out that this only might be an “expansion gap” as aliens showed an increase in both abundance and occupancy with residence time. Occupancy increased faster with time, though, implying that over the centuries, aliens have become more similar to native species in this respect.

Three studies analyzed the distribution patterns of alien species (neophytes) in different European habitats. Cao Pinna et al. (2021) studied the place of origin of 299 neophytes in the Mediterranean biome of Europe. It turned out that as the climatic difference gets smaller and the trade volume with the region of origin gets larger, the relative contribution of neophytes from other biomes increases, showcasing the role of anthropogenic dispersal in filling the potential climatic niche of aliens. Axmanová et al. (2021) provided a comprehensive characterization of neophyte distribution in different types of European grasslands. Generally, European grasslands have a low share of neophytes, with 6.5% of the total species pool being neophytes but only 0.6% of the species occurrences. Among the grassland types, sandy grasslands were most invaded (a quarter of the plots had at least one neophyte), while oromediterranean and alpine grasslands were nearly free of neophytes. Lastly, Wagner et al. (2021) built on a previous study on invasion patterns in European forests (Wagner et al. 2017) to assess the drivers of invasion in more detail. They found that both relative richness and cover of neophytes decreased with elevation and distance to the nearest road or railway, while both metrics increased with the fraction of sealed soil surfaces in the surroundings. However, regions and forest types remained much more important predictors. This finding raises the question of what makes the regions and forest types so different in their susceptibility to neophytes.

Getting more out of databases for macroecology

Macroecology of vegetation can benefit from several global or regional databases of species phylogeny, DNA sequences, distribution, functional traits, interactions, demography, conservation needs and vegetation plots. Using trees as an example and including a range of key distribution and trait databases with genetic and conservation information, Keppel et al. (2021) explored how these sources could be combined. The authors found that even though information coverage for trees is better than for vascular plants in general, genetic, functional, and distribution information is available only for 28% of the 58,000 tree species globally. Data gaps are even more pronounced for functional traits: for the best-covered trait, wood density,

only 13.1% of all species have an entry in open-access databases, while for all the important belowground traits, the coverage is far below 1%.

Večera et al. (2021) used the EVA database to produce maps of plot-based relative species richness per main habitat types (forest, grassland, scrub, wetland) across Europe for a total of 152 vascular plant families. Interestingly, the patterns differed significantly among habitat types. Biurrun et al. (2021) used GrassPlot to derive an aggregated dataset to be used in macroecological studies focusing on the scaling laws of biodiversity and its drivers. The new dataset provides descriptive statistics of species richness of vascular plants, bryophytes, and lichens in grasslands and other open habitats in the Palearctic biogeographic realm at eight different standard grain sizes from 0.0001 to 1,000 m².

Finally, Cutts et al. (2021) explored how printed sources, such as traditional floras, can be used to fill glaring gaps in global databases. Using the Canary Islands as an example, where trait coverage in the plant trait database TRY is very low, they found that estimating specific leaf area (SLA) from entries in the regional flora essentially failed, while it could be well used to derive reasonable values for leaf area.

Resume and outlook

In 1991, Eddy van der Maarel, the founding editor of the *Journal of Vegetation Science*, defined “vegetation science” as “everything the *Journal of Vegetation Science* wishes to publish” (p. 145, van der Maarel, 1991). With the current Virtual Special Issue, we have made a step forward towards ensuring the integration of macroecology into vegetation science. This collection of papers showcases a number of potential topics that the macroecology of vegetation might include, though by no means being an exhaustive list. Patterns of fine-grain plant community characteristics, as well as alpha and beta taxonomic or functional diversity at large spatial extents clearly result as emerging topics. The pace and progress in compiling extensive vegetation plot databases have been staggering. However, big data comes with its own limitations in coverage, quality and accessibility. Several studies outlined some of such imperfections, and there is still much to do to upgrade databases and develop statistical tools. And yet, macroecological vegetation scientists are now in the position to fill many knowledge gaps and tackle urgent global challenges related to the invasion of alien species, changing climate and altered land use. The *Journal of Vegetation Science* has set the stage for such developments and is open for future submissions on the macroecology of vegetation.

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