DOI: 10.17110/StudBot.2025.56.1.155 Studia bot. hung. 56(1), pp. 155–168, 2025

LEVELS OF BIODIVERSITY INSURANCE: SPECIES DISPERSAL, ESTABLISHMENT, FILTERING AND ASSEMBLY IN A CHANGING WORLD – GLIMPSES OF AN ECOLOGIST ENGAGED TO LIMNOLOGY

Péter Török[1, 2, 3] and Béla Tóthmérész[1]

[1]*University of Debrecen, Department of Ecology, H–4032 Debrecen, Egyetem tér 1, Hungary;*
torok.peter@science.unideb.hu, tothmeresz.bela@science.unideb.hu
[2]*HUN-REN-UD Functional and Restoration Ecology Research Group,*
H–4032 Debrecen, Egyetem tér 1, Hungary
[3]*HUN-REN Balaton Limnological Research Institute,*
H–8237 Tihany, Klebelsberg Kuno u. 3, Hungary

Török, P. & Tóthmérész, B. (2025): Levels of biodiversity insurance: species dispersal, establishment, filtering and assembly in a changing world – glimpses of an ecologist engaged to limnology. – *Studia bot. hung.* **56**(1): 155–168.

Abstract: To address the response of ecosystems to global change it is a pivotal task to study the dynamics of communities that structure natural and semi-natural ecosystems. We highlighted new aspects of spatial insurance theory (ecosystem functionality and stability are enhanced by high biodiversity) by introducing three levels of biodiversity insurance: i) landscape-level insurance, ii) habitat-level insurance, and iii) temporal insurance. Based on the above introduced three-level-scheme of biodiversity insurance we identified and summarised several research directions and questions which could be considered in future research. For the better understanding of landscape-level insurance of biodiversity, it is important to quantify the habitat-specific species pools of several terrestrial and aquatic ecosystems, both at the local and landscape-scale. Considering the biodiversity insurance at the habitat level, it is vital to analyse the effect of abiotic and biotic filtering on species and functional diversity both in terrestrial and aquatic communities, and also to analyse how the effects of habitat level filtering processes are influenced by different levels of stress and disturbance. Finally, considering the temporal insurance of biodiversity it is important to determine how species traits interact with temporal biodiversity filters and use that knowledge to predict how species assemblages respond to a range of filter combinations.

Key words: community dynamics, ecological memory, functional trait, intermediate disturbance hypothesis, phytoplankton, spatial insurance

INTRODUCTION

One of the challenges for biodiversity research in the next decades will be to understand the complexity of ecosystem change and resilience at different spatial and temporal scales (IPBES; Díaz *et al.* 2019). To address the response of ecosystems to global change, investigating the dynamics of communities that structure natural and semi-natural ecosystems appears as a pivotal task. However, we are still far from understanding the balance of processes that regulate species filtering and assembly dynamics at local and landscape scales. Focused research that would solve the difficult practical problems frequently occurring in ecological restoration would not only increase our understanding of community assembly and functioning but also would improve the practical implementation of restoration (Török *et al.* 2020).

In the sustainable development goals of the United Nations combatting ecosystems degradation and promoting sustainable management are listed among the highest priorities (United Nations 2019). The United Nations also dedicated the period of 2021–2030 the "Decade of Ecosystem Restoration" fostering that ecological restoration is considered as the most vital and necessary tool to counteract the degradation and to stop and/or mitigate the loss of natural habitats and the decline of biodiversity worldwide (Menz *et al.* 2013, Suding *et al.* 2015). Focused research, which fulfils the needs of both restoration theory and practice is very timely. Research that provides a strong theoretical basis to solve difficult practical problems frequently occurring in ecological restoration would not only improve the practical implementation of restoration but would increase our understanding of community assembly and functioning (Engst *et al.* 2016, Young *et al.* 2005).

Beyond the analyses of species diversity and composition, trait-based functional approaches have become increasingly involved in analysing and explaining the effects of ecosystem processes on functioning. Trait-based functional approaches can help revealing the underlying mechanisms and sustaining diversity and related ecosystem functions (Carmona *et al.* 2012, Tapolczai *et al.* 2016, Viléger *et al.* 2008). The functional approach enables (i) the comparison of ecosystems with quite different species compositions; (ii) making generalizations about dynamic changes in ecosystems caused by altered management, natural disturbance regimes or climate change; (iii) the comparison of assemblages with a high number of taxa; (iv) in the case of taxonomically problematic groups, easier classification than the taxonomic approach, and (v) it also increases the robustness of multivariate statistical analyses by decreasing the number of species axes (Grime and Pierce 2012, Salmaso *et al.* 2015). The use of the trait-based functional approach also enables to compare different ecosystem types, which comparisons might reveal dynamic and functional community attributes which otherwise remain hidden or masked by community-specific processes (Török *et al.* 2016).

With the current paper we are honouring the pioneering work of professor Judit Padisák. One of the key moments of Padisák's work is the recognition and demonstration that the rules of terrestrial community ecology also apply to phytoplankton communities (Padisák 1985). Indeed, phytoplankton assemblages, because of their rapid temporal dynamics, can provide a wealth of new information and theories regarding the rules of organization in terrestrial communities.

Moreover, we can also apply and test the classical theories born in terrestrial ecology in the case of phytoplankton assemblages (Padisák 1996). In the current paper we highlight new aspects of biodiversity insurance theory pointing out which scientific contributions Padisák made to the development of the outlined theories in forms of glimpses of a bright-minded ecologist engaged on limnology. Her creative view of ecological processes, ecological models and theories was manifested at the symposium on succession research organised in Vácrátót in 1983 and was presented in her pivotal contribution (published in Padisák 1985). Later on, the lectures of this conference were published in a book edited by Gábor Fekete (Fekete 1985).

Spatial insurance theory

Spatial dispersal, environmental filtering, biotic interactions, and spatio-temporal stochastic fluctuations caused mostly by disturbance and/or stress determine how species are assembled into local communities from regional species pools (Funk *et al.* 2021, Pärtel *et al.* 2025, Vellend *et al.* 2010). The spatial insurance theory predicts that in a heterogeneous landscape with a diverse regional species pool, local species loss is mitigated; thus, ecosystem functioning is sustained through frequent re-colonisers that replace lost species and maintain high species and functional diversity by metapopulation dynamics (Loreau *et al.* 2003, Shanafelt *et al.* 2015). Incorporating the filtering concept of species assembly (Funk *et al.* 2008, Török *et al.* 2018*a*) we identified three segments of biodiversity insurance operating at different spatial- and/or temporal scales (Fig. 1): (i) landscape-scale insurance, (ii) habitat-level insurance, and (iii) temporal insurance.

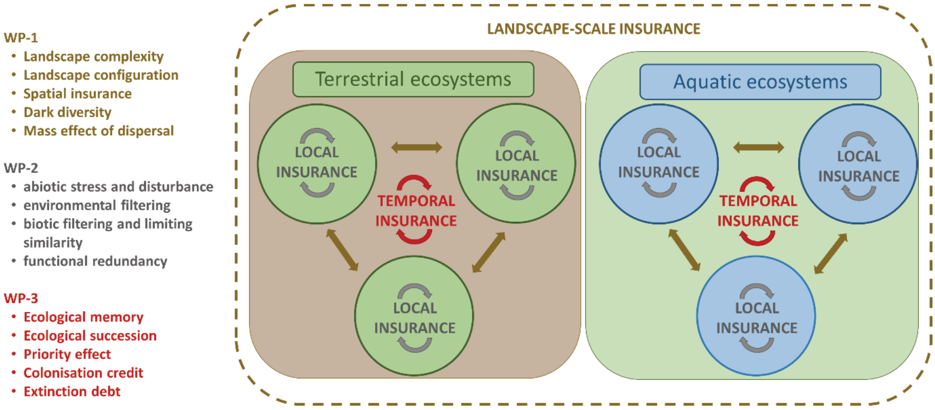

Fig. 1. Relationship between landscape-scale, local, and temporal insurance of biodiversity. Dashed line represents the embedding landscape; the circles are the patches connected to each other mostly by dispersal processes. There are pivotal similarities in the biodiversity supporting processes in terrestrial and aquatic ecosystems instead of critical differences.

Landscape-level insurance

Habitat-scale processes are strongly influenced by the complexity, either composition or configuration of the surrounding landscape in the close or wide proximity of the subjected site. Landscape composition is characterised by the diversity of landscape elements, including natural and semi-natural ecosystems, while landscape configuration focuses on the spatial arrangement of these elements (Tapolczai *et al.* 2021, Tscharntke *et al.* 2012). Focusing on a particular ecosystem, the proximity, connectivity, and abundance and patchiness of landscape elements are especially crucial.

The process of habitat fragmentation involves the subdivision of a continuous habitat patch into several small fragments, the change of spatial configuration habitats, and also an increasing edge effect (Fahrig *et al.* 2011). The increased rate of fragmentation in general decreases the chance of dispersal between identical habitat patches and one of the most important drivers of decreasing diversity (Fahrig *et al.* 2011, Tscharntke *et al.* 2012). Thus, the area of the studied habitat patch, and the quality, quantity, and spatial patterns of its surroundings are crucial to forecast the speed and direction of community change. The species inventory of a given habitat contains species characteristic to the habitat type (habitat specific species pools), but also species characteristic to other habitat types and/or problem species (derived diversity, Török and Helm 2017). The theory of mass effect of dispersal predicts that the composition and diversity of a habitat patch are strongly driven by the immigration of those species whose dispersal units are provided in great abundance in the landscape (Kiemel *et al.* 2023, Leibold *et al.* 2004). Many studies found that higher landscape complexity supports larger habitat-specific species pool, while simple landscapes with high levels of fragmentation and high proportions of man-made habitats may promote the abundance of only a limited number of rather generalist species (Marja *et al.* 2022, Tscharntke *et al.* 2012). However, the effect of landscape complexity is rarely studied in aquatic ecosystems (but see Barbosa *et al.* 1999) or involving multiple ecosystem types (either terrestrial or aquatic) and/or taxa.

Habitat-level insurance

Species establishment is generally driven by environmental filtering caused mostly by abiotic stress. This type of filtering favours species with similar functional characteristics causing trait convergence, especially in highly stressed habitats (Lhotsky *et al.* 2016). Functional redundancy, i.e., the coexistence of species with similar environmental requirements fulfilling the same ecological function in the community is an essential, but rarely validated phenomenon both in terrestrial and aquatic ecosystems (but see Tölgyesi *et al.* 2019 or Várbíró *et al.* 2017).

Increased levels of functional redundancy provide stability to the ecosystems, because species losses do not result necessarily in the loss of functions (Lukács *et al.* 2021, Török *et al.* 2024). Functional redundancy can be considered therefore as local insurance of biodiversity and community functioning. However, species that successfully pass through the environmental filter have quite similar trait combinations, and due to this similarity, they become exposed to strong biotic interactions including competition, which results in biotic filtering. In highly competitive environments, only those species can coexist which differ remarkably in some of their characteristics. Limiting similarity (two coexisting species can have only a limited overlap in their niches) thus promotes trait divergence in these communities and results in functional overdispersion (Várbíró *et al.* 2020). The strength of the environmental or the biotic filtering strongly depends on the abiotic characteristics of the habitats. This assumption is reflected by the stress dominance hypothesis, which states that species and trait-composition is shaped by environmental filtering in harsh environmental conditions (Padisák and Naselli-Flores 2021), while biotic interactions like competition play a pivotal role in the formation of assemblages in resource-rich environments (Csecserits *et al.* 2021). The effect of environmental and biotic filters and thus the trait convergence or divergence in various ecosystems are strongly masked by the disturbance regimes and other biotic interactions; for example, by the suppression of community dominants by grazing (Tóth *et al.* 2016). For the long-term sustainability of biodiversity, it is crucial to understand the small-scale stress-disturbance dynamics related to regeneration niches (Catorci *et al.* 2015). Fine-scale heterogeneity and structurally complex microhabitats may provide more regeneration niches spatially or temporally and allow species to utilize diverse methods to exploit environmental resources at the local scale (Peng *et al.* 2020).

The intermediate disturbance hypothesis (IDH) of Connell (1978) states that species diversity is the highest (maximized) when disturbance is intermediate. IDH is one of the most frequently addressed non-equilibrium models in the ecological literature for explaining the supporting mechanisms of species diversity. In the absence of disturbance competitive exclusion reduces species diversity. In case of intense disturbance only a few species could survive or establish after a disturbance event. When disturbances are intermediate there will be repeated opportunities for the re-establishment of pioneer populations which would otherwise be outcompeted, and the populations of the successful competitors could withstand the disturbance without completely taking over the community. The reason of the success is probably the generality of the IDH; on the other hand, this generality is the reason of several weakness of IDH (Reynolds *et al.* 1993).

Wilkinson (1999) summarized the history of the disturbance and diversity relationship. In terrestrial ecology the idea of disturbance relating to species richness partly originated in the famous paper of WATT (1947). This relationship was demonstrated by a humped back model. This famous graph probably appeared first in Grime's paper (GRIME 1973). Connell's paper demonstrated in a field study the usefulness of IDH explaining the influence of interspecific competition and other factors (CONNELL 1978).

Padisák published an excellent comparison between terrestrial and planktonic communities as a reflection on J. B. Wilson's publication (PADISÁK 1994). Wilson as an eminent plant ecologist focused on the development of terrestrial plant communities of New Zealand (WILSON 1990). PADISÁK (1994) briefly reviewed Hutchinson's plankton paradox and some of the later phytoplankton literature. She summarised the relevance of the IDH in phytoplankton dynamics, assessing its strengths and weaknesses. Finally, she pointed out that the appropriate spatial and temporal scaling of the biodiversity supporting mechanisms are the key issues in understanding community organization.

There is an asymmetry in the history of studying aquatic and terrestrial communities. It was an especially important innovation of Padisák to recognize that it is fruitful to comparatively evaluate of the ecological theories of terrestrial and aquatic ecosystems. Padisák and her co-authors emphasized in an influential paper that the IDH is too useful as a concept to reject and provides a powerful link between diversity and disturbance (REYNOLDS *et al.* 1993). The more robust investigations that are necessary to consolidate the tenancy of IDH need to concentrate on the separation and quantification of the stimulus- and response-components of disturbance (REYNOLDS *et al.* 1993).

The species richness of phytoplankton is discussed by PADISÁK (1993) in the context of CONNELL's (1978) Intermediate Disturbance Hypothesis (IDH) based on a high number of vertical phytoplankton samples obtained from four shallow central European lakes. She provided an explicit estimation of the scale of disturbance. This was especially crucial contribution providing firm data about disturbance (mixing, exceptional meteorological conditions) frequencies of phytoplankton. She demonstrated that less than 3 days can be regarded as high disturbance frequency. Approximately 3-8 days as intermediate disturbance frequency. Larger than 8–9 days means low frequency of disturbance for phytoplankton. Based on real phytoplankton dataset she concluded that her findings support the hypothesis that maximal diversity appears at intermediate disturbance frequencies.

She also demonstrated that the relative importance of intermediate frequency disturbances has its own seasonality: it is increasingly important in periods, in which competition among phytoplankton species is increasing (PADISÁK 1993). This observation provided an opportunity to incorporate the stochasticity-based IDH into more deterministic explanations like PEG-model of SOMMER *et al.* (1986) of plankton succession. PADISÁK (1993) emphasised in this paper that the main difficulty with IDH is that disturbance not only maintains species richness in an ecosystem, but it also supposes its presence. Thus, lack of early or late successional species can inactivate the mechanism of diversity maintenance.

In hydrobiology, Hutchinson's plankton paradox and the IDH are closely related, because these are explaining the mechanisms supporting biodiversity. There are species rich phytoplankton communities in a well-mixed environment, although the species compete for a small number of common limiting resources (HUTCHINSON 1961). In terrestrial plant ecology this paradox is less evident. In a field study Padisák and her co-authors demonstrated that species richness of non-equilibrated lakes was almost three times as high as those in equilibrium (PADISÁK *et al.* 2003). Surprisingly they found that environmental stress (mixing, low light, cold temperatures, high salt content, low level of nutrient) forces phytoplankton communities towards equilibrium, but no relationship between occurrence of equilibria and trophic state was found (PADISÁK *et al.* 2003).

Temporal insurance of biodiversity: succession and ecological memory

The relative importance of different filters and filtering processes in species assembly can vary spatially; however, there is limited understanding of mechanisms mediating the balance of deterministic and stochastic processes temporally (but see TÖRÖK *et al.* 2018*b*). Analysis of patterns in ecological succession, i.e., the spatio-temporal reassembly of natural communities after natural or anthropogenic disturbances, has a long tradition in ecological research (PRACH and WALKER 2019). The study of temporal patterns and processes of community change has also proven fruitful for the research of dispersal mechanisms (SULLIVAN *et al.* 2018), the organisation of various levels of the species pools (FUNK 2021), or in explaining stochastic and priority effects in species establishment (PADISÁK *et al.* 2016, TÖRÖK *et al.* 2018*b*). Ecological processes, including ecological succession are strongly influenced by historical events. Past ecological states and experiences reflected in the form of ecological memory; thus, ecological memory can influence the present or future responses of the community, consequently shaping the dynamic patterns of community integrity and contributing to the trajectory and formation of alternative stable states of an ecosystem (DUPOUEY *et al.* 2002, EGAN and HOWELL 2005).

At the beginning of her carrier Padisák studied the phytoplankton of Lake Balaton on 211 consecutive days between April and November 1980. She found 417 taxa in total during the study period. The number of planktonic species was around 300; majority of the species were extremely rare (PADISÁK 1992). She found that two-thirds of the 300 planktonic species were evenly distributed in time, while the others exhibited temporal peaks. It was especially remarkable that she found that half of the 200 rare species was velocity specialists, able to grow rapidly in spatially and temporally randomly distributed, nutrient-rich microenvironment. She invented a term 'ecological memory' naming the other 100 species of the phytoplankton community, because of the capacity of past states or experiences to influence present or future responses of the community (PADISÁK 1992). This is an important contribution to the understanding of community functioning. The ecological memory is based on the spatial heterogeneity and/or spatial dynamics of the community. The memory of the community comprises all the species which are not completely excluded, i.e. retained in the community because of spatial and temporal heterogeneity.

Ecological memory was defined first as "the capacity of past states or experiences to influence present or future responses of the community" by studying phytoplankton assemblages (PADISÁK 1992). Ecological memory can be also understood as a form of biological legacy, i.e., species resembling past stages of ecosystem composition and development (SUN *et al.* 2013). In terrestrial plant communities seed banks or bud banks are located in the soil, in case of aquatic macrophytes turion banks are in the mud, or cysts or other kind of resting stage formations in many phytoplankton groups can be considered as forms of environmental legacy (e.g., nutrient loads from former disturbances) (SUN *et al.* 2013). The importance of ecological memory in temporal community change is demonstrated by former research both in terrestrial and aquatic communities (OGLE *et al.* 2015, SUN *et al.* 2013). But assessing the magnitude in which ecological memory can influence future changes in species composition and functional trait composition of ecosystems has been lacking. Analysing the relationship between successional processes and ecological memory, and the assessment of the size and diversity of ecological memory may help to explore the priority effect in species dispersal (VON GILLHAUSSEN *et al.* 2014), colonisation credit, and extinction debt theories (BAGARIA *et al.* 2015, KUUSSAARI *et al.* 2009). It also helps to quantify the magnitude of dark- and hidden diversity in various types of ecosystems including both terrestrial and aquatic habitats (PÄRTEL *et al.* 2011, STOOF-LEICHSENRING *et al.* 2012).

Succession research was a favourite topic of botanical research during the last 150 years (FEKETE 1985). Numerous theories and/or models have been developed to interpret and modelling succession processes. The concept of ecological succession is deeply rooted in the study of terrestrial plant communities (CLEMENTS 1916, DRURY and NISBET 1973, GLEASON 1926). This knowledge naturally resulted in the exploration of the rules of community organization from ecological perspective, and finally in the development of ecological models and/or theories explaining community organization (CONNELL and SLATYER 1977). One of the most important characteristics of communities is their species richness. Thus, understanding the rules of community organization, and the mechanisms that maintain biodiversity have become a key issue to the development and accumulation of scientific knowledge. This picture is primarily based on the history of terrestrial vegetation research (Poorter *et al.* 1973).

Ongoing climate change adds another temporal angle of complexity to sustain or restore biodiversity. Novel species pools would include species that are expected to be part of ecosystems under changed conditions (Kasari *et al.* 2016). They can be both natives but also non-natives that are expected to increase/shift their ecological range with changing climate. It may be potentially contentious to start introducing new 'suitable' species during restoration but gaining knowledge of the species and trait composition of novel species pools would allow us to foresee which species are less likely and which species are more likely to persist and contribute to a restored community in the future.

Future perspectives

Based on the above introduced scheme of biodiversity insurance we identified and summarised several research directions and questions which could be considered in future research. For the better understanding of landscape-level insurance of biodiversity it is important to quantify the habitat-specific species pools of several terrestrial and aquatic ecosystems, both at the local and landscape-scale. In particular, it is crucial to focus on answering the questions: (i) How is the local species composition influenced by the patterns, abundance, proximity, and connectivity of habitat patches? (ii) How is the local species diversity of habitats affected by landscape composition and configuration? (iii) How are species groups with different ecological strategies and trait-compositions affected by the different levels of fragmentation and different types of landscape composition? Considering the biodiversity insurance at the habitat level, it is vital to analyse the effect of abiotic and biotic filtering on species and functional diversity both in terrestrial and aquatic communities, and also to analyse how the effects of habitat level filtering processes are influenced by different levels of stress and disturbance. In particular, we can set the questions: (iv) How is the species and functional diversity related to each other in habitats characterised by various levels of stress and/or disturbance? (v) How does environmental filtering affect functional redundancy in ecosystems along a stress and disturbance gradient? (vi) In what magnitude does environmental heterogeneity contribute to the sustainment of high functional and species diversity in various ecosystems? Finally, considering the temporal insurance of biodiversity it is important to determine how species traits interact with temporal biodiversity filters and use that knowledge to predict how species assemblages will respond to a range of filter combinations. Linking the ecological memory concept with ecological succession we identified the following research questions for the future: (vii) What traits or trait combinations favour species being incorporated into ecological memory? (viii) How diverse is the species pool accumulated in form of ecological memory in early, middle, and late stages of ecological succession? (ix) In what magnitude ecological memory contributes to the successional changes of various ecosystems?

A complex trait-based functional approach which explains biodiversity insurance has not been developed so far. It is also a novel aspect to link the functional approach with the understanding of dynamics in community composition which focuses on community functioning based both on compositional changes and ecological traits. This helps to focus practical demand-driven research on community functioning and to redefine several theories explaining colonisation, establishment and assembly with complex multi-scale analyses in terrestrial and aquatic ecosystems.

* * *

Acknowledgements – With the current paper the authors honour the scientific work of Prof. Judit Padisák, highlighting which scientific contributions J. Padisák contributed to the development of the outlined aspects of the spatial insurance theory. The authors thank the support of the National Research, Development and Innovation Office of Hungary (grant numbers: K 137573 and KKP 144068).

Összefoglaló: Az ökoszisztémák globális változásokra adott válaszainak megértéséhez alapvető fontosságú a közösségszerveződés dinamikai folyamatainak vizsgálata. A tájléptékű biztosítás elmélete szerint az ökoszisztémák működése és stabilitása, illetve a tájléptékű biodiverzitás között szoros kapcsolat áll fenn. A közleményünkben a tájléptékű biztosítás elméletét kibontva, a biodiverzitás biztosításának három alkotóelemét ismertetjük: a (i) tájléptékű biodiverzitás-biztosítást, az (ii) élőhelyi szintű biztosítást, és az (iii) időbeli biztosítást. A biodiverzitás tájléptékű biztosításának jobb megismeréséhez ismernünk kell a szárazföldi és vízi ökoszisztémák élőhely-specifikus fajkészletét lokális és tájléptékben is. Az élőhelyi szintű biodiverzitás-biztosítás megértéséhez alapvető az abiotikus és biotikus szűrők a funkcionális diverzitásra gyakorolt hatásának elemzése, és annak értelmezése is, hogy az élőhelyi szintű szűrők működését hogyan befolyásolja a stressz és a zavarás mértéke, valamint ezek kölcsönhatása. A biodiverzitás időbeli biztosítását illetően fontos megvizsgálni, hogy a fajok egyes jellemzői milyen kölcsönhatásban vannak a biodiverzitás időbeli szűrőmechanizmusaival (például a magbankképzés). Mindezek ismerete segíthet abban, hogy előre jelezzük, hogy a közösségek hogyan reagálnak a szűrőfolyamatok minőségében és mennyiségében bekövetkező változásokra.

REFERENCES

Barbosa, F. A. R., Padisák, J., Espíndola, E. L. G., Borics, G. and Rocha, O. (1999): *The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo state, Brazil.* – In Tundisi, J. G. and Straškraba, M. (eds): Theoretical reservoir ecology and its applications. Backhuys Publishers, pp. 425–439.

Carmona, C. P., Azcárate, F. M., de Bello, F., Ollero, H. S., Lepš, J. and Peco, B. (2012): Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. – *J. Appl. Ecol.* **49**: 1084–1093. https://doi.org/10.1111/j.1365-2664.2012.02193.x

Catorci, A., Malatesta, L., Velasquez, J. L., Tardella, F. M. and Zeballos, H. (2015): The interplay of nurse and target plant traits influences magnitude and direction of facilitative interactions under different combinations of stress and disturbance intensities in Andean dry grassland. – *J. Plant Ecol.* **9**: 296–310. https://doi.org/10.1093/jpe/rtv062

Clements, F. E. (1916): *Plant succession: an analysis of the development of vegetation.* – Carnegie Institution of Washington, 498 pp.

Connell, J. H. (1978): Diversity in tropical rain forests and coral reefs. – *Science* **199**: 1304–1310. https://doi.org/10.1126/science.199.4335.1302

Connell, J. H. and Slatyer, R. O. (1977): Mechanisms of succession in natural communities and their role in community stability and organization. – *Am. Nat.* **111**: 1119–1144. https://www.jstor.org/stable/2460259

Csecserits, A., Halassy, M., Lhotsky, B., Rédei, T., Somay, L. and Botta-Dukát, Z. (2021): Changing assembly rules during secondary succession: evidence for non-random patterns. – *Basic Appl. Ecol.* **52**: 46–56. https://doi.org/10.1016/j.baae.2021.02.009

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury, R., Shin, Y. J., Visseren-Hamakers, I. J., Willis, K. J. and Zayas, C. N. (eds) (2019): *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.* – IPBES secretariat, Bonn, Germany, 56 pp.

Drury, W. H. and Nisbet, I. C. T. (1973): Succession. – *J. Arnold Arboretum* **54**: 331–368. https://doi.org/10.5962/p.325716

Dupouey, J. L., Dambrine, E., Laffite, J. D. and Moares, C. (2002): Irreversible impact of past land use on forest soils and biodiversity. – *Ecology* **83**: 2978–2984. https://doi.org/10.1890/0012-9658(2002)083[2978:IIOPLU]2.0.CO;2

Egan, D. and Howell, E. A. (2005): *The historical ecology handbook.* – Island Press, Washington, D. C., 488 pp.

Engst, K., Baasch, A., Erfmeier, A., Jandt, U., May, K., Schmiede, R. and Bruelheide, H. (2016): Functional community ecology meets restoration ecology: assessing the restoration success of alluvial floodplain meadows with functional traits. – *J. Appl. Ecol.* **53**: 751–764. https://doi.org/10.1111/1365-2664.12623

Fekete, G. (ed.) (1985): *A cönológiai szukcesszió kérdései.* – Akadémiai Kiadó, Budapest, 216 pp.

Funk, J. L., Cleland, E. E., Suding, K. N. and Zavaleta, E. S. (2008): Restoration through reassembly: plant traits and invasion resistance. – *Trends Ecol. Evol.* **23**: 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Gleason, H. A. (1926): The individualistic concept of the plant association. – *B. Torrey Bot. Club* **53**: 7–26. https://doi.org/10.2307/2479933

Grime, J. P. (1973): Competitive exclusion in herbaceous vegetation. – *Nature* **242**: 344–347. https://doi.org/10.1038/242344a0

Grime, J. P. and Pierce, S. (2012): *The evolutionary strategies that shape ecosystems.* – Wiley-Blackwell, London, UK, 240 pp.

Kasari, L., Saar, L., de Bello, F., Takkis, K. and Helm, A. (2016): Hybrid ecosystems can contribute to local biodiversity conservation. – *Biodivers. Conserv.* **25**: 3023–3041. https://doi.org/10.1007/s10531-016-1218-3

Kiemel, K., Weithoff, G. and Tiedemann, R. (2023): DNA metabarcoding reveals impact of local recruitment, dispersal, and hydroperiod on assembly of a zooplankton metacommunity. – *Molecular Ecol.* **32**: 6190–6209. https://doi.org/10.1111/mec.16627

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. (2009): Extinction debt: a challenge for biodiversity conservation. – *Trends Ecol. Evol.* **24**: 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. (2004): The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* **7**: 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lukács, Á., Bácsi, I., Nemes-Kókai, Z., Borics, G., Várbíró, G., T-Krasznai, E. and B-Béres, V. (2021): Strong influence of climatic extremes on diversity of benthic algae and cyanobacteria in a lowland intermittent stream. – *Ecohydrology* **14**: e2286. https://doi.org/10.1002/eco.2286

Menz, M. H. M., Dixon, K. W. and Hobbs, R. J. (2013): Hurdles and opportunities for landscape-scale restoration. – *Science* **339**: 526–527. https://doi.org/10.1126/science.1228334

Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., Loik, M. E. and Tissue, D. T. (2015): Quantifying ecological memory in plant and ecosystem processes. – *Ecol. Lett.* **18**: 221–235. https://doi.org/10.1111/ele.12399

Padisák, J. (1985): *A fitoplankton szukcessziója.* – In: Fekete, G. (ed.): A cönológiai szukcesszió kérdései. Akadémiai Kiadó, Budapest, 216 pp.

Padisák, J. (1996): *Szukcesszió és diverzitás sekélytani fitoplankton társulásokban.* – MTA Dokt. ért.

Padisák, J. (1992): Seasonal succession of phytoplankton in a large shallow lake (Balaton, Hungary): a dynamic approach to ecological memory, its possible role and mechanisms. – *J. Ecol.* **80**: 217–230. https://doi.org/10.2307/2261008

Padisák, J. (1993): The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. – *Hydrobiologia* **249**: 135–156. https://doi.org/10.1007/BF00008850

Padisák, J. (1994): Identification of relevant time-scales in non-equilibrium community dynamics: conclusions from phytoplankton surveys. – *New Zeal. J. Ecol.* **18**: 169–176.

Padisák, J. and Naselli-Flores, L. (2021): Phytoplankton in extreme environments: importance and consequences of habitat permanency. – *Hydrobiologia* **848**: 157–176. https://doi.org/10.1007/s10750-020-04353-4

Padisák, J., Borics, G., Fehér, G., Grigorszky, I., Oldal, I., Schmidt, A. and Zámbóné-Doma Z. (2003): Dominant species, functional assemblages and frequency of equilibrium phases in late summer phytoplankton assemblages in Hungarian small shallow lakes. – *Hydrobiologia* **502**: 157–168. https://doi.org/10.1023/B:HYDR.0000004278.10887.40

Padisák, J., Vasas, G. and Borics, G. (2016): Phycogeography of freshwater phytoplankton: traditional knowledge and new molecular tools. – *Hydrobiologia* **764**: 3–27. https://doi.org/10.1007/s10750-015-2259-4

Pärtel, M., Szava-Kovats, R. and Zobel, M. (2011): Dark diversity: shedding light on absent species. – *Trends Ecol. Evol.* **26**: 124–128. https://doi.org/10.1016/j.tree.2010.12.004

Pärtel, M., Tamme, R., Carmona, C. P., Riibak, K., Moora, M., Bennett, J. A. et al. (2025): Global impoverishment of natural vegetation revealed by dark diversity. – *Nature* **641**: 917–924. https://doi.org/10.1038/s41586-025-08814-5

Peng, M.-H., Hung, Y.-C., Liu, K.-L. and Neoh, K.-B. (2020): Landscape configuration and habitat complexity shape arthropod assemblage in urban parks. – *Sci. Rep.* **10**: 16043. https://doi.org/10.1038/s41598-020-73121-0

Prach, K. and Walker, L. R. (2019): Differences between primary and secondary plant succession among biomes of the world. – *J. Ecol.* **107**: 510–516. https://doi.org/10.1111/1365-2745.13078

Poorter, L., Amissah, L., Bongers, F., Hordijk, I., Kok, J., Laurance, S. G. W., Lohbeck, M., Martínez-Ramos, M., Matsuo, T., Meave, J. A., Muñoz, R., Peña-Claros, M. and van der Sande, M. T. (2023): Successional theories. – *Biol. Rev.* **98**: 2049–2077. https://doi.org/10.1111/BRV.12995

Reynolds, C. S., Padisák, J. and Sommer, U. (1993): Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. – *Hydrobiologia* **249**: 183–188. https://doi.org/10.1007/BF00008853

Salmaso, N., Naselli-Flores, L. and Padisák, J. (2015): Functional classifications and their application in phytoplankton ecology. – *Freshw. Biol.* **60**: 603–619. https://doi.org/10.1111/fwb.12520

Sommer, U., Gliwicz, Z. M., Lampert, W. and Duncan, A. (1986): The PEG-model of seasonal succession of planktonic events in fresh waters. – *Arch. Hydrobiol.* **106**: 433–471. https://doi.org/10.1127/archiv-hydrobiol/106/1986/433

Stoof-Leichsenring, K. R., Epp, L. S., Trauth, M. H. and Tiedemann, R. (2012): Hidden diversity in diatoms of Kenyan Lake Naivasha: a genetic approach detects temporal variation. – *Mol. Ecol.* **21**: 1918–1930. https://doi.org/10.1111/j.1365-294X.2011.05412.x

Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B. and Schwartz, K. Z. S. (2015): Committing to ecological restoration. – *Science* **348**: 638–640. https://doi.org/10.1126/science.aaa4216

Sullivan, L. L., Clark, A. T., Tilman, D. and Shaw, A. K. (2018): Mechanistically derived dispersal kernels explain species-level patterns of recruitment and succession. – *Ecology* **99**: 2415–2420. https://doi.org/10.1002/ecy.2498

Sun, Z., Ren, H., Schaefer, V., Lu, H., Wang, J., Li, L. and Liu, N. (2013): Quantifying ecological memory during forest succession: a case study from lower subtropical forest ecosystems in South China. – *Ecol. Ind.* **34**: 192–203. https://doi.org/10.1016/j.ecolind.2013.05.010

Tapolczai, K., Bouchez, A., Stenger-Kovács, C., Padisák, J. and Rimet, F. (2016): Trait-based ecological classifications for benthic algae: review and perspectives. – *Hydrobiologia* **776**: 1–17. https://doi.org/10.1007/s10750-016-2736-4

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. and Westphal, C. (2012): Landscape moderation of biodiversity patterns and processes - eight hypotheses. – *Biol. Rev.* **87**: 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Tölgyesi, C., Török, P., Kun, R., Csathó, A. I., Bátori, Z., Erdős, L. and Vadász, C. (2019): Recovery of species richness lags behind functional recovery in restored grasslands. – *Land Degrad. Dev.* **30**: 1083–1094. https://doi.org/10.1002/ldr.3295

Török, P. and Helm, A. (2017): Ecological theory provides strong support for habitat restoration. – *Biol. Conserv.* **206**: 85–91. https://doi.org/10.1016/j.biocon.2016.12.024

Török, P., T-Krasznai, E., B-Béres, V., Bácsi, I., Borics, G. and Tóthmérész, B. (2016): Functional diversity supports the biomass-diversity humped-back relationship in phytoplankton assemblages. – *Funct. Ecol.* **30**: 1593–1602. https://doi.org/10.1111/1365-2435.12631

Török, P., Helm, A., Kiehl, K., Buisson, E. and Valkó, O. (2018*a*): Beyond the species pool: modification of species dispersal, establishment, and assembly by habitat restoration. – *Restor. Ecol.* **26**: S65–S72. https://doi.org/10.1111/rec.12825

Török, P., Matus, G., Tóth, E., Papp, M., Kelemen, A., Sonkoly, J. and Tóthmérész, B. (2018*b*): Both trait-neutrality and filtering effects are validated by the vegetation patterns detected in the functional recovery of sand grasslands. – *Sci. Rep.* **8**: 13703. https://doi.org/10.1038/s41598-018-32078-x

Török, P., Bullock, J. M., Jiménez-Alfaro, B. and Sonkoly, J. (2020): The importance of dispersal and species establishment in vegetation dynamics and resilience. – *J. Veg. Sci.* **31**: 935–942. https://doi.org/10.1111/jvs.12958

Török, P., Teleki, B., Erdős, L., McIntosh-Buday, A., Ruprecht, E. and Tóthmérész, B. (2024): Scale dependency of taxonomic and functional diversity in pristine and recovered loess steppic grasslands. – *Sci. Total Environ.* **949**: 175110. https://doi.org/10.1016/j.scitotenv.2024.175110

Tóth, E., Deák, B., Valkó, O., Kelemen, A., Miglécz, T., Tóthmérész, B. and Török, P. (2016): Livestock type is more crucial than grazing intensity: traditional cattle and sheep grazing in short-grass steppes. – *Land Degrad. Dev.* **29**: 231–239. https://doi.org/10.1002/ldr.2514

United Nations (2019): *United Nations Decade of Ecosystem Restoration 2021–2030. A/RES/73/284.* Resolution adopted by the General Assembly on 1 March 2019. – https://docs.un.org/en/A/RES/73/284

Várbíró, G., Görgényi, J., Tóthmérész, B., Padisák, J., Hajnal, É. and Borics, G. (2017): Functional redundancy modifies species–area relationship for freshwater phytoplankton. – *Ecol. Evol.* **7**: 9905–9913. https://doi.org/10.1002/ece3.3512

Várbíró, G., Borics, G., Novais, M. H., Morais, M. M., Rimet, F., Bouchez, A., Tapolczai, K., Bácsi, I., Usseglio-Polatera, P. and B-Béres, V. (2020): Environmental filtering and limiting similarity as main forces driving diatom community structure in Mediterranean and continental temporary and perennial streams. – *Sci. Total Environ.* **741**: 140459. https://doi.org/10.1016/j.scitotenv.2020.140459

Villéger, S., Mason, N. W. and Mouillot, D. (2008): New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* **89**: 2290–2301. https://doi.org/10.1890/07-1206.1

von Gillhaussen, P., Rascher, U., Jablonowski, N. D., Plückers, C., Beierkuhnlein, C. and Temperton, V. M. (2014): Priority effects of time of arrival of plant functional groups override sowing interval or density effects: a grassland experiment. – *PLoS ONE* **9**: e86906. https://doi.org/10.1371/journal.pone.0086906

Watt, A. S. (1947): Pattern and process in the plant community. – *J. Ecol.* **35**: 1–22. https://doi.org/10.2307/2256497

Wilkinson, D. M. (1999): The disturbing history of intermediate disturbance. – *Oikos* **84**: 145–147. https://doi.org/10.2307/3546874

Wilson, J. B. (1990): Mechanisms of species coexistence: twelve explanations for Hutchinson's paradox of the plankton. – *New Zeal. J. Ecol.* **13**: 17–42.

Young, T. P., Petersen, D. A. and Clary, J. J. (2005): The ecology of restoration: historical links, emerging issues and unexplored realms. – *Ecol. Lett.* **8**: 662–673. https://doi.org/10.1111/j.1461-0248.2005.00764.x

(submitted: 03.08.2025; accepted: 12.09.2025)