

## Non-equilibrium thermodynamics and development cycles of temperate natural forest ecosystems

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### Abstract

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The presented contribution in its first part summarizes several important theoretical findings of the system ecology supporting non-equilibrium paradigm of complex adaptive systems. We emphasise the concept of non-equilibrium thermodynamics of living systems and the Holling's adaptive cycle of a social-ecological system. In natural forests, the phases of an adaptive cycle fit to a substantial extent also to stages and phases of a large and a small forest cycle, although there is a different terminology. Further, we have emphasised the natural role of disturbances and their explanation from the thermodynamic point of view – as an important component of an adaptive cycle, which supports conclusions that these natural phenomena not only participated in the evolution of the whole habitats, but from the long-term view, they may even increase the resilience and overall ecological stability of ecosystems. Finally, we have tried to apply the findings of the theories presented to derive or underlie several principles of the management of temperate deciduous and mixed natural forests, which we consider important.

### Keywords

adaptive cycle, natural forest, non-equilibrium thermodynamics, resilience

### Introduction

Forests are an irreplaceable phenomenon of the Earth. They are crucial for stabilizing the global ecosystem, e.g. they contain the largest stocks of carbon in their biomass; therefore deforestation, forest degradation, and regeneration are globally crucial for the carbon cycle (PAN et al., 2011). The forests provide many other ecosystem services supporting human health and quality of human life. Apart from this, forests provide habitats for substantial part of the world terrestrial plant and animal taxons (HASSAN et al., 2005). The ecological importance of forests ecosystems is generally respected, but opinions on them differ considerably (VYSKOT, 2003).

Forests ecosystems naturally change over time, but today they have been increasingly influenced by the processes of deforestation, fragmentation, degradation, pollution, overhunting (and illegal hunting for bushmeat, PRIMACK et al., 2011), spread of invasive species and climate change. In degraded forests, ecological processes driving forest dynamics are diminished or strongly limited (GHAZOU et al., 2017).

Central and Eastern Europe has still a relatively high proportion of natural or close-to-nature forests (MIKUSINSKI and ANGELSTAM, 1998; BADEA et al., 2004; APPLETON and MEYER, 2014). In natural forests, their original (or close to original) species composition has been preserved. They have a character of primeval forests (with differentiated

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spatial structure and substantial age and thickness variability, KORPEL, 1989). Primeval forests are probably the most important forest ecosystems (APPLETON and MEYER, 2014). Basic features of natural forests, preferentially dealt with in this paper, include persistence of their species composition (mainly the native woody plants, results of phylogenetic development in post-glacial age, KORPEL, 1991), maintenance of relative ecological autonomy and ecological balance (conditioned by specific internal forest climate, its dynamics and stabilized soil processes, KORPEL, 1989), adequate size, varied age (conditioned by naturally differentiated lifespan of trees and longer renewal).

Currently, many forests in Europe, including the Carpathian forests, face significant changes, loss of biodiversity, reducing of abundance and vanishing of many threatened and vulnerable species, partial loss of canopy, etc. (ANFODILLO et al., 2008; KUEMMERLE et al., 2009). The main causes of forest degradation include synergy of climate change, worsened health state of the forests, intensification of their use, but also insufficient perception of the high complexity of living systems (PROULX, 2007) which naturally move towards higher complexity (MICHENER et al., 2001). HEYLIGHEN (1999) recognises structural (spatial) and functional (behavioral) complexity. Forest complexity is a product of multiple and diverse interactions between populations of species and of their interactions with the environment. These result also in new, emergent ecosystem properties (e.g. biodiversity, resilience) and high nonlinearity of ecosystem dynamics (LEVIN, 1998).

Forests are subject to various cyclical changes of their age profile, spatial structure and species composition (PTRETZSCH, 2008), induced mainly by ecological conditions of the biogeographical region and its woody plants composition (influenced by ecological and competitive properties of plants, their growth dynamics, span of life, etc.). Identification of changes in their composition and structure is critical for comprehension of how these ecosystems react to the changing conditions of environment (RUNKLE, 2000; URIARTE et al., 2004; WOODS, 2000). As knowledge of forests complexity, including temperate forests, grows, a new non-equilibrium paradigm of natural systems emerges (PLESNIK, 2018). Classical ecology was based on the idea that ecosystems are usually in a close and predictable equilibrium with various factors of environment, which are only sparsely disturbed by interventions from outside. This was expressed in the endeavour of the managers of natural resources to achieve and conserve „*equilibrium in nature*“. During the 1980s and 1990s the concept of ecological stability was established in Central Europe (MICHAL, 1994; VOLOŠČUK, 2001). However, despite existence of a climax stage, a final ecosystem state, which we should conserve for ever, does not exist (ROHDE 2006, in PLESNIK, 2010). Ecosystems are liable to ceaseless and hardly predictable changes and their dynamics is better expressed by a metaphor of „*flowing mosaic of habitats*“ (PLESNIK, 2010). This metaphor is driven by a non-equilibrium concept. The aim of this paper is presentation of applying the concept of non-equilibrium thermodynamics

to the small forest development cycles theory, to emphasize the important role of natural disturbances in the forest dynamics.

## Methods

We focused on the dynamics of European temperate primeval forests, especially in the central part of Europe, including the Carpathians, and we interpreted it within the prism of non-equilibrium thermodynamics and Holling development cycle. For this purpose, we conducted an intensive literature search to gather certified data and concepts in order to compare and interconnect these two issues. Especially Web of Science journals, but also other major journals and books have been reviewed. Finally, this allowed us to stress an important ecological role of natural disturbances and to derive a few proposals for sustainable management of temperate natural or close-to-nature forests.

## Small and large forest development cycles

The dynamics of temperate forests is usually described by well-known models of a small and large forest cycles. The large forest cycle includes cyclical changes of the dominant woody species (Fig. 1), running after large-area dieback of codominant trees (HART and CHEN, 2006). Due to a large serious natural disturbance, even natural catastrophe, the former tree layer is removed, and the large-area encompassing restoration phase starts with a pioneer forest. The pioneer woody species are later replaced by shade-loving ones and a new stage is formed – a transitory forest. The development is headed towards a climax forest, or in special conditions into unevenly age-differentiated stands (SCHMIDT-VOGT, 1991).

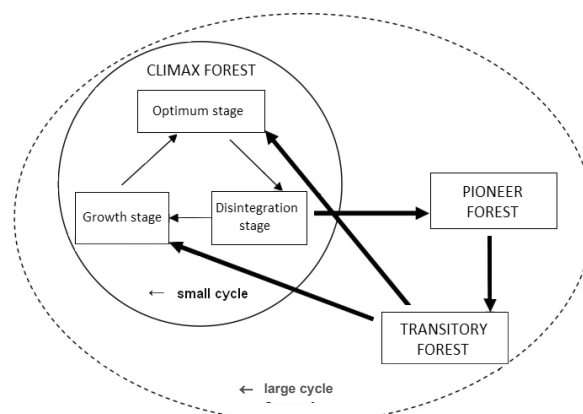


Fig. 1. The small and large cycles of forest development. According to KORPEL, 1989; MICHAL, 1992.

A small forest development cycle (Fig. 1) was described for mixed natural Central European forests (e. g.

RUBNER, 1925; LEIBUNDGUT, 1959; KORPEL, 1989). This cycle is divided into three basic development phases. As we observe them within a framework of a continual development, the first phase of a climax forest is continuously following the pioneer forest stage and is followed by the phase of growing-up climax woody species (ČABOUN, 2000). Characteristic ones are mostly trees of younger generations, intensively utilizing their growth capabilities. The forest stand is distinguished by counterbalancing positive and negative relations, which leads to a high ecological stability, especially to ecological resistance of the ecosystem, but still with a substantial fitness for its dynamic development.

The adult phase (optimum stage from the point of view of production) lasts from culmination of the vertical growth of trees, to culmination of the girth growth. The forest stands achieve maximal stocks. The cessation of the vertical growth leads to levelling out the originally vertically differentiated stands. There is a small number of trees in the spatial unit, mortality of the biggest trees increases and the canopy is moderately loosened. The structure of the forest is strongly levelled-out vertically and its physiognomy is similar to a horizontally connected even-aged forest (KORPEL, 1989). These forests, with maximum accumulated biomass amount have a high resistance (due to superiority of positive relations), but smaller resilience. At the end of this phase, the adult trees start ageing. The tree stocks quickly decreases, as dying of the vigorous trees cannot be replaced by increasing accretion of remaining living trees, neither by individuals of a new generation. The static stability decreases, the ecosystem lost also its ecological resistance.

On released sun-lit areas, there starts a renewal of shade-loving climax woody species. This is the regeneration or juvenile phase. Young trees have considerable resilience – the ability to adapt to new conditions or to cope with negative effects of external factors. The resistance of the ecosystem is rather low, but during succession it increases. The cyclic, non-linear development of natural forest emphasises the fact that, in reality, the climax stage in such a forest is replaced by a mosaic of individual development phases. Individual forest patches may be found at different phases of ecosystems development cycle, formed by species-different plant and animal communities. In this view, a natural forest can be understood as a flowing mosaic of various stages and phases of the development cycle (ČABOUN, 2000). The dynamics of forest ecosystems, together with changes of land use, strongly influences also ecosystem services (SMAIL and LEWIS, 2009).

### **The concept of non-equilibrium thermodynamics of living systems**

The driving force for all life processes, also in forest ecosystems is energy. According to the thermodynamic theory of living systems (JØRGENSEN and SVIREZHEV, 2004), biological and ecological complexity represents a spontaneous response of a living system to a certain rela-

tively stable environment (e.g. climate, soils, hydrology) and to a certain amount of energy, in order to utilise this energy and other natural resources at best, which is called “*a maximum power principle*” (ODUM, 1977; JØRGENSEN, 2012).

This trend of increasing structural and functional complexity can be observed in ecological succession and in biological evolution (ADAMI et al., 2000; WÜRTZ and ANNILA, 2010). It results from the system’s tendency to utilize at best the available free high-quality energy (KAY, 2000). This explains, to a certain extent, also the exceptional complexity (and biodiversity) of tropical rainforests. For example, the research on pollen history in the lowland Amazonian forest demonstrates that the tropical rainforest occupied this region continuously even during the last glacial maximum, despite the fact that the temperatures were lower by 5 °C to 6 °C (COLINVAUX et al., 1996). It may be concluded that long-lasting favourable climate enabled development of a large genepool which fuelled further evolution.

The development of living systems towards a higher complexity is in seeming conflict with the Second law of thermodynamics, according to which each transformation of energy in a closed system increases its entropy and thus causes the system disorder. This conflict is resolved by the concept of non-equilibrium thermodynamics of living systems (JØRGENSEN et al., 2007), based on the Prigogin’s non-linear dynamics of dissipative structures (PRIGOGINE, 1997).

The answer is that each living organism, ecosystem or social-ecological system is truly relatively closed from its organizational point of view, but at the same time it is a thermodynamically open system fuelled by an input of high quality energy. According to the thermodynamic theory of living systems (JØRGENSEN and SVIREZHEV, 2004) this input of energy drives the system further from the point of thermodynamic equilibrium with its environment. To cope with the energy gradient, a system is compelled to process the received energy, i.e. to convert it, while using a part of it to build up its internal organization (KAY, 2000). Another part of this energy is dissipated into energy of lower quality (mainly as a waste heat). In this way, dissipative structures and processes of a forest ecosystem spontaneously increase and maintain its internal organization at the expense of entropy production and export. The higher is the input of energy, the more complex dissipative structures and processes the system develops (if other resources are sufficient, in terrestrial ecosystems mainly humidity and nutrients).

The dynamics of the forest stand structure in natural, but also semi-natural forest, is guided by the processes of autoorganization (including autoregeneration), which lead to new dissipative structures and by the processes of autoregulation, which maintain the developed structures and processes. The dynamic interplay of these two groups of processes keeps the ecosystem alive. Dynamic equilibrium of the relations between individual components of a natural ecosystem allows its long-term existence even on

poor soils (KORPEL, 1989).

In this context, also thermodynamic model of a succession is appropriate: During ecological succession, biomass accumulates in an ecosystem, thus changing its energy balance (WÜRTZ and ANNILA, 2010). The living part of ecosystem, biocoenosis, is compelled to respond to this new available free energy – by developing new, more complex dissipative structures and processes (KAY, 2000). This is manifested in distinct successional changes of the species composition due to development of new trophic chains using more of available energy. During succession, the amount of used and preserved high-quality energy grows (JØRGENSEN et al., 2007), which leads to origin of new niches, arrival of new species and their specialization. In this way, thermodynamics explains, why during succession the abundance of r-strategists recedes and the abundance of K-strategists increases, as this allows a more efficient use of the available resources. Thermodynamics also explains why the biodiversity of natural forests increases during their long-term evolution: according to JØRGENSEN (2012), the energy available to ecosystems is naturally utilized in three main ways: 1) in building more biomass, 2) in enhancing networks, e.g. interaction networks among the species and thus also biodiversity, 3) in enhancing information.

### Holling adaptive cycle of ecosystem development

Forest ecosystems, including temperate forests, are complex adaptive systems (LEVIN, 1998), developing towards higher complexity and subordinated to the laws of thermodynamics (KAY, 2000). In this context, there is relevant a model of adaptive cycle of ecological (and social-ecological system) phases, called a Holling cycle (HOLLING, 2001). This cycle is based on alternating two long-term phases, in which maximal production (in phase r) or conservation (in phase K) is achieved, and two short-term phases in which disruption of old organization (in phase  $\Omega$ ) is a necessary step before the renewal of the system, its reorganization can be realized (in phase  $\alpha$ ). This model suggests that complexity of living systems emerges due to a relatively small number of „critical processes“, which create and maintain the system’s self-organization (HOLLING, 2001, Fig. 1).

The exploitation phase r in forests is characterized by a maximum growth and, especially at its beginning, by high interspecific competition and colonization of unoccupied territories by r-strategists. During the conservation phase K, the ecosystem further accumulates energy and matter, but accretions are lower, with emerging more new niches. This explains an increase in K-strategists during succession, with populations achieving the limits of the ecosystem carrying capacity, and the system is in the climax stage. It can be said that the ecosystem in this phase, due to accumulated supplies of energy, is waiting for disturbance (e.g. fire, windstorm, insect outbreak, disease). A natural disturbance triggers the phase  $\Omega$ , which means an abrupt disruption of the organization achieved in phases r and K. However, this disruption is

„creative“, as it releases resources accumulated during the phases r and K (e.g. energy bound in the wood of trees). A phase  $\alpha$  of rapid reorganization follows, in which conditions for entering the system into a new phase r develop, and the whole cycle repeats again (HOLLING, 2001, 2004). It should be noted, that sometimes these disturbances occur before an ecosystem reaches the K phase, but they are less common and they have smaller impact – due to a smaller amount of energy accumulated in the biomass.

The adaptive cycle is characterized by the following four key features (HOLLING, 2001), Fig. 2:

1. Its potential, i.e. „wealth as expressed in ecosystem structure, productivity, mutations, ... and inventions“ denotes an inherent potential for change, which increases incrementally in the phases r and K, while simultaneously increasing also the system rigidity.
2. As the potential grows, „slow changes gradually expose an increasing vulnerability (decreased resilience)“ towards disturbances. A disturbance triggers a release of the accumulated potential as a „creative destruction“ in a back loop from K to  $\Omega$ .
3. In the reorganizational phase  $\alpha$  innovations occur „when uncertainty is great, potential is high, and controls are weak, so that novel recombinations can form“. A low connectedness allows development of new unexpected combinations of innovations.
4. The innovations are tested: „Some fail, but others survive and adapt in a succeeding phase of growth from r to K“.

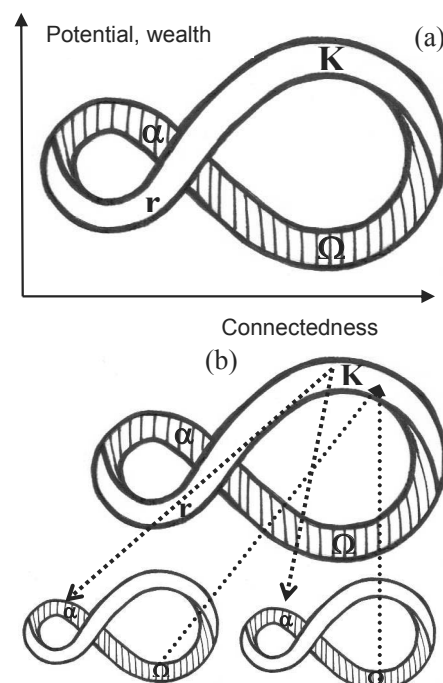


Fig. 2. Adaptive cycle (a), ecosystem development framed by potential and internal connectedness; the concept of panarchy (b), nesting of adaptive cycles of lower hierarchies into hierarchically higher cycles. According to GUNDERSON and HOLLING, 2002, adapted.

We should mention the soft differences between Holling's resilience and ecological stability. Ecological stability expresses the ability of ecological system to balance spontaneously outer disturbances and to „*preserve and reproduce their substantial characteristics*“, its most important components are ecological resistance and ecological resilience (MÍČAL, 1994, 1998). The international organization Resilience Alliance defines resilience as “*the capacity of a social-ecological system to absorb or withstand perturbations and other stressors such that the system remains within the same regime, essentially maintaining its structure and functions*” (GUNDERSON and HOLLING, 2002). Another definition of “*engineering resilience*” takes into account the time required by ecosystem to return to pre-disturbance state, the shorter this time, the more resilient ecosystem is (PIMM 1984). Therefore Resilience Alliance and Pimm's definitions together cover both resistance and resilience aspects of ecological stability, but maybe they better reflect high ecosystem dynamics.

Finally, the Holling cycle enhances also our understanding of hierarchy. Analogically as lower hierarchical structures are nested and integrated into higher ones (e.g. cells into tissue, species into ecosystem), also the Holling's adaptive cycles at lower hierarchical levels are nested and integrated into hierarchically higher adaptive cycles. This hierarchy of living systems, which includes objects, processes and cycles, is called panarchy (HOLLING, 2001; GUNDERSON and HOLLING, 2002). The concept of panarchy in fact enhances the notion of hierarchy by its dynamic component – nesting of never ending adaptive cycles.

### Applying Holling adaptive cycle to temperate forests dynamics

When compared, the phases of a Holling cycle correspond to a considerable extent to phases of the development cycles of natural forests: „*a large cycle*“, which prevails mainly in dynamic processes in boreal forests characterized by secondary succession and large disturbances, and „*a small cycle*“, realized within climax, i.e. a specific case of cenotically stable geobiosphere the woody plants of which exist in longer time period in relatively balanced proportions (Fig. 1c.)

In forest cycles, three relatively ordered groups of processes alternate. The first one is growth of trees, leading to biomass accumulation. The second one is their consequent dieback, understood as a consecutive decrease of living biomass in a forest ecosystem, and finally there are regeneration processes which safeguard interconnection of the processes of dieback and growth and alternating generations of natural forest (PALUCH, 2007).

The phases of Holling's cycle correspond to the phases of temperate forest development cycles as follows:

1. The exploitation phase  $r$  expressed by tree growth corresponds to the phase of transitory forest in the large cycle and to the stage of growing up in the small cycle.
2. The conservation phase  $K$  corresponds to the phase of climax forest in the large cycle, with decreased accumulation of biomass, and to the stage of optimum in the small cycle.

3. The release phase  $\Omega$  corresponds to the disintegration (breakdown) stage of the small cycle, expressed by a dieback of trees, with resulting gaps within the forest stands.
4. The reorganization phase  $\alpha$  to a certain extent corresponds to the phase of pioneer forest in the large cycle and to reorganization processes in the small cycle which interconnect destruction stage and growing up stage. The important difference is that in the Holling's cycle, these reorganization processes form a unique, distinctively expressed phase.

„*A creative destruction*“ in the phase  $\Omega$  is fundamental for ecosystem reorganisation in the phase  $\alpha$  and its redevelopment in phases  $r$  and  $K$ . This we consider as a crucial contribution of the Holling cycle to understand the forest dynamics. Concerning natural or close-to-nature forests, this means that the order, extent and character of regeneration processes are conditioned by the natural lifespan of the main woody species (SANIGA and BRUCHÁNIK, 2009) and their dieback.

Also the phenomenon of panarchy is clearly visible also in temperate natural forests developing in relatively closed integrated cycles (with superior dynamic cyclic development of woody components). The structure of these forests depends on their patch history, especially species composition, and age profile and changes during the development cycle. In this cycle, various forest stand structures alternate, from intricately differentiated (by height, thickness, area) to simple. Permanent multilayer structure is more exceptional and it is bound to certain woody species, habitat conditions and energy inputs (KOŠULIČ, 2010). Differences in forest structure influence development processes in association with development stages and phases. Forest texture accentuates spatial mosaic of development stages and their phases in a larger spatial extent (KORPEL, 1991). The size of the mosaic patches and the overall areal proportion of development stages and development phases, over the whole forest area, are good indicators of the ecological balance between growth and development processes, stability and permanent autonomy of a natural forest (KORPEL, 1989).

The forest cycle concept traditionally used in European forestry research has also been assessed as being generally too simplistic (CHRISTENSEN et al., 2007; GRATZER et al., 2004; KRÁL et al., 2018) and this concept has been questioned several times at using quantitative spatial analyses, looking for non-random ‘patchy’ arrangements of growth and mortality processes (SZWAGRZYK and SZEWCZYK, 2001), or by finding close-to-random stand characteristics on the finest spatial scales in natural spruce–fir–beech forests (PALUCH, 2007; PALUCH et al., 2015). Our answer is that both sides of this seeming conflict are true, as living systems are characterized by both deterministic and stochastic processes (JØRGENSEN et al., 2007). And it is just a combination of firm biological and topological rules and accidents (disturbances) that keeps ecosystems close to „*the edge of chaos*“ (PARROTT, 2010).

## Disturbances within the framework of non-equilibrium thermodynamics

Disturbances, i. e. calamities, mainly windstorms, gradations of bark beetles, wood destructive fungi, frost, snow cover, long term drought, fires, etc. belong to key factors influencing the natural forest development. In the sense of the definition by PICKETT and WHITE (1985), these are any discrete events disturbing the structure of ecosystems, communities or populations and changing the resources, substrate or physical environment, while they are natural or anthropogenic. Each disturbance is characterized by its type, extent, intensity, frequency of occurrence and significance of its impacts. These characteristics are influenced by land cover, heterogeneity, abiotic conditions and presence of barriers in landscape (FORMAN and GODRON, 1993). Disturbances of intermediate extent and intensity even increase the species diversity in community, as they suppress dominant species and improve conditions for competitively weaker species (*intermediate disturbance hypothesis*, CAIN et al., 2014).

Each disturbance in ecosystem creates a new environment, which includes “*a biological legacy*”. This includes all the surviving organisms and dead individuals, preserved in the place after the disturbance had passed away, as well as new structures (FRANKLIN et al., 2007). Biological legacy is crucial for ecosystem processes and biodiversity, as it supports regeneration processes, increases the level of resilience and helps many taxons to survive and to stay in the disturbed areas, or it provides new niches to be occupied by new species. Disturbances create a substrate for novelties emerging in the regeneration phase  $\alpha$ . Protection of biodiversity and ecosystems is essentially linked to the way we deal with this biological legacy, i.e. how we manage the localities after disturbance. Instructions of natural forests say that these have been preserved in places which were not further disturbed by humans and where their biological legacy was preserved, enabling the ecosystem regeneration into the pre-disturbance state.

Natural disturbances in natural forests lead to dying of individual trees and the whole forest stands. Smaller disturbances initialize a regeneration process mainly in the woody component of the forest ecosystem (within the small forest cycle). In natural forests, one of the decisive mechanisms safeguarding alteration of growth and breakdown stages is the origin of forest stand gaps, important for the start of the processes of natural regeneration. Their creation in forests stands with originally continuous canopy invokes dynamic phenomena known as „*gap regeneration*“ (RUNKLE, 1981), “*patch dynamics*” (PICKETT and WHITE, 1985) or „*gap dynamics*“ (VAN DER MAAREL, 1988). Dieback of one or more trees due to their expired lifespan or due to a small natural disturbance leads to origin of small gaps accompanied by creation of conditions for start of natural renewal in a new succession (WHITMORE, 1978; YAMAMOTO, 2000). Long-term outcome of these processes is the shifting mosaic of various successional stages of the forest.

Although it has been acknowledged that this phenomenon exists also within natural forests in Central Europe (KORPEL, 1995), it is commonly assumed that the fine-scale disturbances are the principal natural pathway for canopy recruitment in most forests dominated by late-successional species (e.g. KORPEL, 1982, 1989, 1995; SPLECHTNA and GRATZER, 2005; SPLECHTNA et al., 2005). Small and intermediate natural disturbances not only create conditions for the system reorganization (CARPENTER and GUNDERSON, 2001), but from a long-term view, these disturbances even increase the system resilience (as well as ecological stability).

Again, thermodynamics can be used to explain this: In the climax forest stage (conservation phase K), the accumulation of energy is already so extensive, that the system is waiting for a disturbance triggering a sudden release of energy (phase  $\Omega$ ), bound mainly in the wood. Thanks to high accumulation of energy during ecosystem development, the ecosystem can respond by developing new dissipative structures (mainly during succession) and by enhancing its dynamics through new dissipative processes. This is characterised by variability and rate of the change of ecosystem individual phases. For example, in the small forest cycle, the release phase is represented by dieback of individual trees, triggered by narrowly localized disturbances, while in the large forest cycle, the release phase is triggered by large disturbances, e.g. fires, windstorm, bark beetle gradations, etc. Therefore, from a long-term perspective, there exists also an important ecological role of even such “*forestry enemies*”, as are the bark beetles.

A substantial role of disturbances is to disrupt the existing system organization in order to release the accumulated energy. Although many organisms die during this process, in the following post-disturbance regimes, many niches are renewed and even new ones are created. The dissipative structures and dissipative processes are reorganized, which is supported by the energy release, but also by recycling matter, seed bank formation in soil and by other biological legacies of the ecosystem (FRANKLIN et al., 2007). This new environment fulfils a number of functions in the ecosystem, stirs regeneration processes and contributes to the ecosystem resilience.

Small and medium disturbances contribute to the resilience in temperate natural (or close to nature) forest ecosystems, as these disturbances lead to a flowing mosaic of various successional stages. Paradoxically, such a natural forest has a substantially higher resilience and resistance than the climax seminatural forest with a continuous canopy – as a natural forest is a lively mosaic of forest stands being in r, K,  $\Omega$  and a phases of the Holling cycle. The concept of panarchy (HOLLING, 2001; GUNDERSON and HOLLING, 2002) implies that the stability of hierarchically higher ecological system (in this case a forest whole) is generated by relatively high dynamics of its hierarchically lower components (forest patches in different phases of development and species populations in different phases of their oscillations). The smaller are the patches with structural differences, the smoother is the development of

the natural forest whole which achieves a higher ecological stability and more balanced dynamics even in case of a smaller overall area. On the contrary, if the dynamics of the lower hierarchy is weaker, i.e. it is realized over larger areas and by slower processes, the ecological stability will be lower, even in case of larger overall area. Therefore, the size of the individual patches, uneven age differentiation, and overall areas and dynamics of the individual development phases are good indicators for the equitability of growth, breakdown and regeneration processes, thus also for the ecological stability, permanent autonomy and functionality of a natural forest (ČABOUN, 2000).

Numerous studies deal with relations of biodiversity to resilience and ecological stability. This affair is not clear, although some studies point to a positive relation between the biodiversity and ecosystem stability (WANG and LOREAU, 2016). On the other hand, contributions of species to ecosystem functionality are different, the most important being the keystone species. However, even other species may be significant from the long-term point of view. Extinction of species decreases the ecosystem functionality unless their freed niches are occupied by species with similar functional roles (OLIVER et al., 2015). This phenomenon is based on a functional redundancy of some species and it increases the ecosystem resilience. Resilience is simultaneously also a measure of adaptability of ecosystem towards changed ecological conditions (FOLKE et al., 2004; ALLEN and HOLLING, 2010). It is important that resilience enables also to stabilize ecosystems functions and ecosystem services.

We summarize that disturbances in forest ecosystems represent natural processes participating in the evolution of the whole habitats. From the anthropocentric point of view, they seem to be negative (especially in commercial forests), but from the point of view of evolution, these disturbances are a part of complex dynamics, underlying survival, vitality and adaptability of the ecosystem biota. From the long-term point of view, the legacy of disturbances can even increase the resilience of the ecosystem structure, species composition and overall functionality of the system.

### Several recommendations for management of natural or close-to-nature forests

In case of management of natural or close to nature forests – possible to differentiate according to several criteria, there are generally two fundamental options (the realization of which currently leads to numerous discussions and polemics):

1. To leave the disturbance-impacted forest stand to natural processes exclusively (i.e. without forestry interventions). This management mode should be applied in natural forests in large core zones of national parks, or in national reserves with sufficient buffer zones.
2. To perform forestry interventions known from commercial forests. But also in this case “*forest management close to nature*” should be applied (SANIGA and BRUCHÁNIK, 2009).

Considering the complexity theory, especially non-equilibrium thermodynamics and adaptive cycles, we supply and underline several recommendations for (not just natural) forest management:

1. Be aware of forest ecosystem complexity as a condition of its vitality: Complexity is a natural and typical feature of ecosystems organization (LEVIN, 2005) tending to increase during their development and evolution. Each natural ecosystem has its natural level of complexity at which its vitality is the highest. This complexity might be generated by interactions between a variable environment and internal ecosystem organization (ANAND et al., 2010). Therefore, natural complexity can be supported through measures leading to a higher habitat and species diversity and, at the same time, preserving or renewing the original ecological processes. Higher complexity also supports multiple ecosystem services.
2. Be aware of biodiversity as an ecosystem insurance: Current global changes may cause that some species marginal in ecosystem today may become important in the future. High biodiversity allows replacement of eventually extinct species with those that have similar functional roles in the ecosystem (OLIVER et al., 2015). The functional redundancy serves as an insurance against the ecosystem collapse after an abrupt or widespread change of its outer environment (PLESNIK and VAČKÁŘ, 2005). On the opposite, a biodiversity loss increases the risk of origin of extinction cascades – it has been proved that species extinction combined with low functional redundancy leads to a domino effect of many other extinctions (SCIENCEDAILY, 2018).
3. Be aware of high ecosystem dynamics and disturbances: Growth and conservation phases, as well as breakdown and reorganization phases are definite part of high ecosystem dynamics (GUNDERSON and HOLLING, 2002). If the forest is in the phase K (climax stage), then the arrival of a disturbance triggering a release of the energy bound in the wood of trees is a matter of time. Disturbances (in the breakdown stage or release phase  $\Omega$ ) lead to temporal changes in the biota composition, water and nutrient resources. However, human post-disturbance interventions may further disrupt abiotic and biotic processes, increase ecosystem vulnerability to disturbances, deplete biodiversity, increase risk of invasions and loss of biological legacies, interfere with natural population recoveries, increase risks of ecosystem collapse, etc. (LINDENMAYER et al., 2017).
4. Be aware of a climate change as a massive change to the outer environment: The climate change is a reality and it will transform forest ecosystems. There is expected a large shift of vegetation zones from the equator towards the poles, a shift of vegetation belts towards higher altitudes, changes to the species areals and their phenology – which altogether may lead to a number of trophic mismatches, changes in number of abiotic ecological conditions, etc. (examples are listed e.g. in

EEA, 2017). Many forest ecosystems may be altered and may not be resilient and resistant enough to cope with the climate change (THOMPSON, 2011). In Europe, this is already valid for spruce ecosystems, with their thermal optimum today in many places beyond the conditions of their actual environment. As areals of many species will change and shift, it is necessary to improve the connectivity across full range of habitats to support the future migrations.

5. Be aware of increase in ecological stability as a necessary management goal: According to ROCKSTRÖM et al. (2009) anthropogenic pressures on the Earth System have achieved a level when an abrupt global change cannot be excluded. Destabilized global climate system already leads to more windstorms, insect outbreaks, droughts, fires. We cannot stop them, but we could increase especially the resilience of the forests (and in this way also ecological stability). The concept of panarchy (GUNDERSON and HOLLING, 2002) is a good start, as “stability” of hierarchically higher systems is based on high dynamics of the lower ones. In species rich primeval forests this is provided by floating mosaic of different phases of the adaptive development forest cycles. Even the managed close to nature forests may be transformed into a floating mosaic of smaller patches differing by individual phases. In this way, we support natural adaptability of ecosystems to changes, i.e. their natural responses to disturbances, which mostly is not possible to estimate and compensate adequately (GELATIČOVÁ and Šibík, 2015).
6. Be aware of ontic openness and surprises, apply adaptive management: Ecosystems have certain patch dependency (LEVIN, 1998) and they follow certain organizational rules of their development. On the other hand, their high complexity, non-linearity and irreversibility of processes means a high level of indeterminism, with posing limits to our knowledge of these systems and predictability of their behaviour (KAY, 2000). The ontic openness of ecosystems described by JØRGENSEN (2012) and others enables the ecosystems regeneration, but this may lead to surprises, to unexpected new ecosystem states. Therefore, the response to ontic openness of forest ecosystems should be in adaptive management.

## Conclusions

Temperate forests are complex adaptive systems developing towards higher complexity, while being subordinated to laws of thermodynamics. Both the classical model and thermodynamic-approach model represent development of natural (and close to nature) forests in relatively closed cycles. In the first one, alternation of the development and breakdown stages is safeguarded by three interrelated processes: the growth of trees leading to biomass accumulation, their consecutive dieback and retreat of living biomass, and regeneration processes linking the processes of dieback and growth.

In natural forests, the crucial mechanism backing up this alteration is the origin of forest stand gaps and adjacent processes of natural regeneration. The thermodynamic approach (Holling cycle) distinguishes four phases (exploitation, conservation, release and regeneration) pointing especially to the ecological importance of natural disturbances in forest development (energy release phase), and sets apart a unique reorganization phase. Disturbances disrupt the ecosystem organization and release the energy accumulated during the development phases. In the following post-disturbance mode, the dissipative structures of the ecosystem are reorganized, utilising the released energy, recycled matter and genetic information from the surviving species, seed bank and other biological legacies. From the anthropocentric point of view, these processes may be considered negative (especially in commercial forests), but from the evolutionary point of view, they form a natural complex ecosystem dynamics, which is a necessary condition for ecosystem survival, development and adaptability. From the long-term view, disturbances represent „investments into future”.

Small disturbances initialize mainly the processes of regeneration of the woody component of the forest ecosystem (small development cycle) and, at the same time, these processes support the resilience and resistance of hierarchically higher entities within the framework of the large development cycle. According to the concept of panarchy, it is just nesting and integration of many small forest cycles into a large one, which safeguards the ecological stability of the forest as a whole.

We hope that new questions opened by quickly developing theories of system ecology, especially by non-equilibrium thermodynamics and adaptive ecosystem cycles, may lead to a better understanding of forests and thereafter to their more effective management.

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