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Adaptability and functional stability in forest ecosystems: a hierarchical conceptual framework

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In this paper we present a hierarchical conceptual framework to study adaptability and functional stability of aggregate functions across scales in forest ecosystems in the face of environmental variability with special reference to temperate trees. Natural ecosystems display a range of adaptive responses to environmental changes, including differential gene activity and phenotypic plasticity (individual-level mechanisms), differential reproduction of genotypes (population-level mechanisms), and changes in species abundances (community-level mechanisms). We examine which of these responses are typically observed in temperate forests under changing environmental conditions. Following hierarchical adaptability theory, we regard adaptation as a never-ending multilevel hierarchical process of individual-, population- and community-level adjustments to a constantly changing environment. Adaptive adjustments at all organizational levels tend to stabilize aggregate ecosystem properties such as primary production and nutrient cycling. We propose that approximately the same plasticity limits hold for long-lived forest trees and the community of short-lived soil microorganisms. The rate of adaptive rearrangements, however, differs greatly between organisms: we suggest that a year for microorganisms is equivalent to a millennium for trees. Therefore, the forest tree communities are expected to adjust to multi-year climate oscillations as easily as microorganisms to seasonal variability. Such adjustments are made possible by increased expression or proliferation of pre-adapted genes, genotypes, and species.

Key words: hierarchical adaptability theory, plasticity, genotypic diversity, species diversity, climate change

INTRODUCTION

Recent biodiversity experiments have provided evidence that species diversity enhances the functional stability of ecosystems (Hooper et al., 2005; Tilman et al., 2006; van Ruijven, Berendse 2007; Isbell et al., 2009; Hector et al., 2010). The stabilizing effect of species diversity results from the fact that different coexisting species are complementary in their responses to environmental fluctuations (McNaughton, 1977; Yachi, Loreau, 1999; Loreau, 2010): as long as environmental conditions change within usual limits, some species for which these environmental conditions are favourable are likely to be present. The increased biological activity of these species compensates for the decreased activity or growth of other species from the same community (Gonzalez, Loreau, 2009) so that functional stability of aggregate community properties is achieved. In other words, species in a community are pre-adapted to a range of usual environmental changes.

Functional properties of populations in turn can be stabilized due to another component of biodiversity, i. e. genotypic diversity. An environmental

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change that is unfavourable to some genotypes may be favourable to others. Thus, some genotypes may compensate for decreased activity in others. A number of authors (Endler, 1977; Mátyás, 1996; Davis, Shaw, 2001; Kelly et al., 2003; Hamrick, 2004; Jump et al., 2006; Thompson, 2009) maintain that trees and shrubs possess quite a rich diversity of genotypes pre-adapted to climate warming or other environmental changes.

Phenotypic plasticity is yet another mode of adaptation, which has received much less attention from ecologists and forest managers. Individual adaptation mechanisms are widespread among plants (e. g. Larcher, 2003) and may be used by plants when responding even to considerable environmental changes. For instance, it has been established that a tree's optimal temperature for photosynthesis can fluctuate by several degrees Celsius depending on air temperature (Gunderson et al., 2010). Forest trees are often considered to be rather plastic as during their lifetime, which can exceed several hundred years, they are forced to adapt to a great many drastic changes in the environment, including periods of heat and drought.

Thus, under the impact of climate change or any other disturbance, a forest ecosystem may display the following adaptive responses: migration (1), evolution (2), shifts in the abundance of pre-adapted species (3), shifts in the frequency of pre-adapted genotypes (4), and phenotypic plasticity (5). However, it is currently unclear whether all these responses are accessible to forest communities.

The main objective of this article is to present a hierarchical conceptual framework that allows elucidating which of these adaptive responses or strategies are typically displayed by temperate forests under changing environmental conditions. We mainly focus, however, on the latter three modes of adaptation. Here we use "adaptation" in the broad sense of the term, i. e., as any mechanism that results in improved performance after an environmental change. We also use the term "adaptive strategy" in a broad sense, without necessarily implying any form of higher-level selection. Following hierarchical adaptability theory (HAT) (Conrad, 1983; Lekevičius, 1986; 2011b) we regard adaptation as a multilevel hierarchical process that is constantly at work under natural conditions. In this view, individual-level mechanisms of adaptation are nested within population- and community-level mechanisms. To the best of our knowledge, HAT has not been used for a similar purpose so far.

We present a general conceptual framework of adaptability in temperate forests that could be used for modelling purposes, but we do not attempt here to turn this framework into a comprehensive mathematical model of all adaptive transformations, from biochemical changes to species sorting. Such a comprehensive model will be difficult to build because adaptive transformations occur at multiple hierarchical levels and there is currently a shortage of appropriate data, especially on interactions between adaptive mechanisms. Our conceptual framework can reveal tendencies and provide some qualitative predictions, but we do not use it to provide quantitative predictions about adaptation in current forests. Our approach inevitably combines elements from both the inductive or empirical approach (elements derived from data) and the deductive or theoretical approach (elements derived from HAT). We view this dual approach as a first step toward building a more predictive, quantitative theory, the predictions of which could be tested by experiments.

Terminology is often a problem when building a conceptual model. In this article, we do our best to specify the use of such frequent concepts as adaptation, adaptability, adaptation rate, tolerance and plasticity limits, seasonal selection, species sorting, year-to-year selection, and genetic load. Some of these concepts have been used differently and quite freely by various authors in recent years, what has resulted in considerable confusion over terminology. We also seek to demonstrate that most of these concepts can be successfully used not only for the description of evolutionary, biochemical and physiological adaptation, but also for that of adaptive population- and community-level rearrangements. Not only individuals, but also populations and communities have specific means for adjustment to routine environmental changes, and our study demonstrates that adaptation can proceed at all organizational levels simultaneously.

In section 2 we first summarize the main elements of HAT. We believe this information is necessary because recent developments of the theory have been made in languages other than English.

In sections 3 and 4 we then use HAT and the insurance hypothesis (Yachi, Loreau, 1999; Loreau, 2010) to examine the adaptive responses of temperate forest communities to diurnal, seasonal, year-to-year and longer-term fluctuations in climatic conditions. Finally, in section 5 we discuss the potential for temperate forests to adapt to current climate change. We conclude that forests are likely to be pre-adapted to some degree to changing climate conditions.

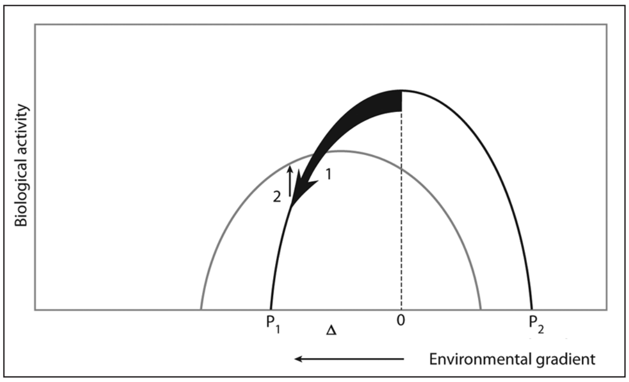

Fig. 1. The response of organisms to an environmental gradient may be represented by a shift of tolerance curves. O is an optimum and P_1 and P_2 are two pessima. Biological activity decreases (1) following an abrupt worsening of environmental conditions (Δ), but it may be partly or wholly restored after some time due to adaptation (2). Following Lekevičius, 1986

SOME ELEMENTS OF HIERARCHICAL ADAPTABILITY THEORY (HAT)

Hierarchical Adaptability Theory defines adaptation as the process by which a decline in biological activity (growth, reproduction, primary production, etc.) induced by environmental changes is restored (Conrad, 1983; Lekevičius, 1986). That is quite a broad treatment of the adaptation concept. It encompasses not only evolution, but also reversible rearrangements on the level of an individual, population or community, in cases when these transformations ensure survival and functional stability.

According to HAT, the various levels of adaptation form a hierarchy. This means that populations have a richer repertoire of responses than do the individuals that constitute them: they can respond to environmental changes not only through phenotypic plasticity, but also through changes in genotype frequency. Ecological communities have an even richer repertoire as they can adapt to environmental changes not only through individual-level phenotypic plasticity and population-level genotypic diversity, but also through changes in species abundances made possible by species diversity. Therefore, aggregate ecosystem properties, such as total biomass, primary production, and nutrient cycling efficiency, should be most buffered. Local nutrient cycles ensure the long-term viability of the whole ecosystem, including primary producers.

In an ecological context, adaptation is a process by which individuals, populations and entire communities can adjust to ever-changing environmental conditions (Fig. 1).

A distinction should be made not only between the direct impact of an environmental change (arrow 1 in Fig. 1) and the response to this change (arrow 2 in Fig. 1), but also between tolerance and plasticity (Lekevičius et al., 2011). Tolerance can be assessed by placing organisms in different environmental conditions and immediately measuring their biological activity. This allows quantifying the direct impact, not adaptation. To assess plasticity, changes in the environment should be brought about slowly enough or, if they are abrupt, biological activity should be measured after a long enough period of time that the organism can adjust to these changes. There is no limit to the number of potential tolerance curves for an organism or a population as these curves can shift depending on the direction of environment changes. In contrast, as plasticity curves are recorded in genetic material, they can shift only during the course of evolution. The same holds true for the limits of tolerance and plasticity. These represent the range of environmental conditions within which organisms can survive and reproduce, depending on whether the environment changes rapidly (limits of tolerance) or slowly (limits of plasticity). To be more exact, the limits of plasticity are the limits within which pessimal points slide along an environmental gradient (Fig. 1). These limits, which are defined by the reaction norm, should always be broader than the limits of tolerance. The slower the rate of environmental changes, the greater the potential for adaptation, *ceteris paribus*.

As a result of routine changes in environmental conditions, some structures (and related functions) lose their optima, whereas others gain them. The former structures disintegrate or their activity is inhibited; the latter multiply and their associated functions are strengthened. For example, an elementary or enzymatic function can be strengthened in the following ways: (1) the enzyme concentration in a cell increases; (2) the number of cells carrying this enzyme grows due to mitosis; (3) the frequency of genotypes producing this enzyme increases; or (4) the population itself grows. One of the strengths of this theory is that it predicts the existence of a considerable number of reserve structures (e. g. "silent" and weakly transcribable genes, rare genotypes, and rare species). These reserve structures can be viewed as a form of memory about past events, as hidden information, part of which occasionally resurfaces whenever environmental conditions require it.

The ability to adapt, or adaptability, comprises two components: adaptation rate and plasticity limits (Lekevičius, 1986, 2011). Adaptation rate can be viewed as the rate at which tolerance curves shift along the environment gradient. The faster the adaptation rate and the broader the plasticity limits are, the greater the adaptability of an individual, population or community is. Although the adaptation rate of individual-level mechanisms is fastest, these mechanisms operate only within a comparatively narrow range of environmental conditions. Thus, they ensure comparatively narrow plasticity limits. In contrast, although evolutionary mechanisms operate very slowly, they make it possible to adapt to virtually all conditions. Population- and community-level mechanisms lie somewhere between these two extremes. In short, there is a trade-off between adaptation rate and plasticity limits, which arises from the fact that adaptive rearrangements are restricted by different factors at different levels of organisation. The rate at which individual-level mechanisms operate is controlled by the rates of molecule synthesis and cell multiplication (in a multicellular organism). The rate of population- and community-level rearrangements is restricted by generation time and fertility. The rate of evolution is restricted not only by generation time and fertility, but also by the rate of mutagenesis and the frequency of recombinations. Therefore, the process of evolution is generally very slow.

FOREST PLANTS AND SOIL MICROORGANISMS EMPLOY DIFFERENT STRATEGIES FOR ADAPTATION TO FLUCTUATIONS IN ENVIRONMENTAL CONDITIONS

Forest organisms inhabit environments that have many dimensions (temperature, precipitation, etc.), each of which varies temporally and spatially. Temporal fluctuations can occur over short or long timescales, and on each timescale, variation can be regular (e. g. diurnal and seasonal patterns of environmental changes, perhaps some multi-year oscillations) or irregular. The distribution of abiotic fluctuations can be viewed as having a fixed mean and variance, at least in the short term.

Let us consider rearrangements that enable temperate forests to adjust to more or less regular environmental fluctuations, such as diurnal, day-to-day, and seasonal. HAT predicts that all organisms co-existing in the same locality are characterized by the same adaptability as they are under the effect of a similar variability of abiotic conditions (Conrad, 1983). However, the mechanisms employed by organisms to adapt themselves to this variability differ. For instance, during their lifetime mature trees growing in a certain forest and the community of soil microorganisms dwelling under those trees are likely to have experienced roughly similar changes in the abiotic environment (although the soil is a much buffered medium compared with the atmosphere). Both trees and microorganisms were forced to respond to all these changes in one way or another. The fact that trees and soil microorganisms have survived shows that they had a sufficient repertoire of responses at their disposal, although their responses must have differed in character. During the course of their ontogenesis, trees could respond only by changing their phenotype within the limits of their inherited reaction norm, while the microbial community, in addition to this mechanism, had the possibility of changing their population abundance and the frequency of pre-adapted genotypes. Over several decades or hundreds of years microorganisms might have managed to make use of evolutionary mechanisms, which was probably impossible in the case of trees. Despite the difference in the strategies used, the end result was the same – survival regardless of environmental instability.

The gene pool of any natural population stores a great deal of information on environmental changes that the population has experienced in the past (Conrad, 1983; Lekevičius, 1986; Lekevičius et al., 2011). Therefore, any change in the environment within the usual range induces a corresponding response. The repertoire of these responses has likely been built up by natural selection. This explains the fact that adaptation to ordinary changes in the environment as a rule does not require genetic changes. New genetic information becomes indispensable only when extraordinary changes occur in the environment.

Let us imagine forest trees in the age range of 100–200 years standing nearby. During their lifetime they have experienced nearly the same changes in abiotic environment as the organisms that decompose forest litter and other organic waste in the soil underneath them. Although possibly determined by different mechanisms, the plasticity limits of these trees and of their coexisting soil organisms should be approximately the same. Yet the generation time of trees may be as long as several decades; that of small animals is most often measured in weeks or months; and that of soil microorganisms (bacteria, archaebacteria and protists) normally does not exceed a few hours or, more rarely, a few days (Barcenas-Moreno et al., 2009). These differences in generation time account for differences in their specific adaptation strategies (Fig. 2). It was merely through phenotypic plasticity (i. e. the norm of reaction determined by an individual genotype) that trees could adapt to environmental fluctuations that occurred over the period of tree growth. Meanwhile, the community of soil microorganisms could respond to these changes not only at the cellular level, but also by changing genotype frequencies in populations and population sizes in communities. All these changes were, supposedly, reversible, just like the abiotic changes demanding adaptation to them. Whatever changes occur in the environment, they induce the appearance of appropriate pre-adapted structures, e. g. genes, genotypes, or species. This is because environmental conditions in a particular locality have been fluctuating within a similar range for hundreds or thousands of years, and hence natural selection has had enough time to accomplish its task.

Phenotypic plasticity involves behavioural, biochemical and physiological mechanisms. To adapt to environmental changes within the ordinary limits, organisms usually employ two biochemical mechanisms, i. e. "qualitative" and "quantitative" ones (Hochachka, Somero, 2002). Qualitative mechanisms involve transcription of the genetic information stored in the hitherto "silent" loci. By contrast, quantitative mechanisms involve changes

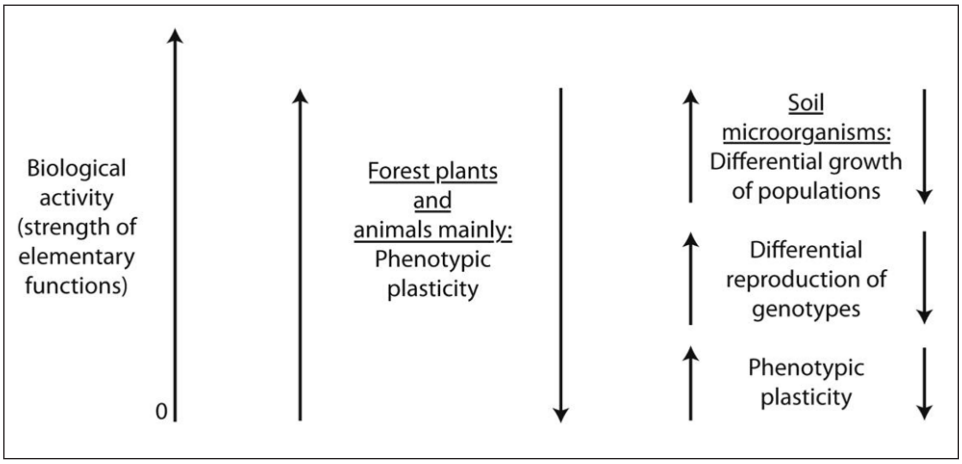

Fig. 2. Likely responses of the main components of a temperate forest ecosystem to diurnal, day-to-day, and seasonal fluctuations in abiotic conditions. Elementary functions are enzymatic functions, and their reinforcement is due to biosynthesis, mitosis and reproduction of organisms (for further explanations see section 2)

in the concentration of enzymes and metabolites in a cell as well as in the number of cells containing the necessary enzymes or metabolites. Both these mechanisms seem to be typical of most, perhaps even all, plants, microorganisms and animals (Hochachka, Somero, 2002; Larcher, 2003). For instance, when a summer heat wave strikes a certain locality, C_3 – plants acclimate by slowing respiration, stimulating electron transport capacity, and synthesizing a thermostable isoform of Rubisco activase (Sage, Kubien, 2007).

Some studies (Zogg et al., 1997) have shown that seasonal changes in soil temperature induce corresponding transformations in microbial communities: populations of mesophilic bacteria and fungi increase in summer, while those of psychrophilic bacteria increase in late autumn and winter. Experiments conducted on fungal and bacterial communities in arable soil of South Sweden revealed that incubation temperature vs growth rate curves has the ability to shift (Bárcenas-Moreno et al., 2009), thus probably allowing temperature optima to adjust to temperature changes in the field. A similar phenomenon was also observed in silt bacteria (King, Nedwell, 1984). King and Nedwell (1984) called this phenomenon "seasonal selection", although they did not study changes in genotype frequencies. To avoid confusion, it seems reasonable to use a different term, such as selective population growth, species sorting (Bárcenas-Moreno et al., 2009), or seasonal succession, which is widely used by hydroecologists. The issue is not merely one of terminology: according to HAT, differential population growth in microorganism communities should be always accompanied by genotype frequency fluctuations in adapting populations and by biochemical adaptation mechanisms in each individual within these populations. The latter two mechanisms are constituent parts of the first one and are also means for accomplishing subtler optima adjustment.

Differential genotype multiplication (Fig. 2) caused by seasonal changes in environmental conditions was first observed in insects, and later in protists and planktonic crustaceans (for survey see e. g. Lekevičius, 2007). This phenomenon was called seasonal selection. The essence of this phenomenon is that different genotypes respond differently to temperature, light, humidity and other abiotic environmental factors. Hence, under seasonal changes in the environment, the frequency of genotypes varies periodically. For instance, cold-preferring genotypes reproduce in early spring and autumn, while heat-preferring genotypes reproduce in summer. According to HAT, changes in genotype frequencies should be accompanied by phenotypic changes, as individual adaptation mechanisms are constituent parts of population-level mechanisms. This hypothesis is supported by a study of adaptation to seasonal temperature in rotifers (King, 1972). It is noteworthy that, although seasonal selection is apparent, there is no evolution because frequencies merely fluctuate around certain mean values. This response often lasts for a month or longer because generation time in rotifers and many other small invertebrates is several days at least and fecundity is not very high (Gurevičiutė et al., 1989). Unfortunately, to date we have no direct evidence that seasonal selection occurs in soil microorganisms. However, heterogeneity of soil microorganism populations is very likely (e. g. Belotte et al., 2003; Kassen, Rainey, 2004; Grundmann, 2004), as is the fact that their polymorphism is sustained by the variability of environmental conditions (Kassen, Rainey, 2004).

What impact can such seasonal rearrangements in microorganism communities exert on forest ecosystems? Some authors (Verville et al., 1998; McHale et al., 1998; Liski et al., 1999; Rustad et al., 2001; Luo et al., 2001) maintain that such rearrangements contribute to the stabilization of soil microorganisms' functions, in particular community respiration and organic matter decomposition. Artificial soil heating causes a temporary increase in respiration, which later, however, reverts to its initial level (McHale et al., 1998; Rustad et al., 2001). Thus, within a certain range, this function becomes temperature-independent.

Although forest plants adapt to diurnal, day-to-day and seasonal fluctuations in environmental conditions mainly through phenotypic plasticity, this does not mean that genotypic and species diversity does not perform any stabilizing role. Due to their long generation time, seasonal selection is not accessible to plants. However, genetic diversity with respect to response to temperature, humidity, light and other abiotic factors is present in tree populations (Endler, 1977; Mátyás, 1996; Hamrick, 2004; Thompson, 2009). Many tree species have a large number of forms and varieties differing in phenology and morphology (Mátyás, 1987; Savolainen et al., 2004). Populations of woody plants are more heterogeneous in this respect than those of herbaceous plants (Hamrick, 2004). For instance, investigation of phenological differences among individuals in a *Pinus sylvestris* population revealed that the difference between the dates of growth termination in autumn is up to several dozens of days (Mátyás, 1987). Some authors (Vavrek et al., 1996) suppose that this kind of within-population diversity in plant populations is transmitted from one generation to the next and is sustained by seasonal and year-to-year changes in environmental conditions (mainly, in temperature, precipitation and light), as well as spatial patchiness of environmental conditions. This diversity is also likely to stabilize population-level biomass and productivity, both temporally and spatially.

The abiotic niches of different coexisting tree species generally differ as well, in a way that the growth of some species may be favoured in cold (or damp) years and that of others in warm (or dry) years (Ellenberg, 1988; Kozlowsky et al., 1991; Larcher, 2003). Species diversity is expected to stabilize the aggregate functional properties of plant communities because different species have different responses to environmental fluctuations (McNaughton, 1977; Yachi, Loreau, 1999; Hooper et al., 2005; Tilman et al., 2006; van Ruijven, Berendse, 2007; Isbell et al., 2009; Hector et al., 2010; Loreau, 2010). For example, when temperature optima differ among species, temperature fluctuations within a certain range are unlikely to significantly affect primary production because whatever the change in temperature within this range, some species in the community will benefit from this change.

SHOULD FOREST TREE COMMUNITIES ADAPT TO MULTI-YEAR OSCILLATIONS AS EASILY AS MICROBIAL COMMUNITIES ADAPT TO SEASONAL VARIABILITY?

Forest trees produce a lot of seeds per hectare annually. Merely a small part of them sprout up, an even smaller part of seedlings get established, and only a few trees reach maturity. Hence, selection in tree populations, as a rule, is quite intense (Endler, 1977; Le Corre, Kremer, 2003). Trees are predominantly outcrossed, so nearly every individual is unique. A study of one *Betula pendula* population (Kelly et al., 2003) revealed that the genotypes selected from those present in the youngest cohorts vary with different years: some genotypes have better chances of sprouting, getting established and surviving in colder years, others in warmer years. Hence, some age groups are dominated by genotypes specific to cold years, others by genotypes typical of warm years. Seedlings are most vulnerable to climatic factors in their establishment phase. Therefore, in later developmental stages, genotypes specific to warm years are not eliminated even in colder years. As seedlings containing these different genotypes grow side by side, the hypothesis that they were selected by spatial peculiarities of environmental conditions seems hardly plausible.

This type of selection could be referred to as year-to-year selection (Fig. 3). Stabilizing selection may easily become directional annually, although in a year or two this direction reverses to the opposite one. Changes in genotype frequencies in a cohort should be accompanied by both physiological and biochemical rearrangements because of the hierarchy of adaptation mechanisms. Later, when plants get established, individual mechanisms become the only possible mode to adapt to diurnal, seasonal, and year-to-year fluctuations. As the difference between the mean temperatures of relatively warm and cold summers is about 1 °C or slightly larger, genotypes specific to "cold years" and "warm years" presumably can overcome it by means of phenotypic plasticity.

As the period of climatic oscillations increases, there should appear the possibility of altering genotype frequency not only in certain-age cohorts, but also in the whole population. If the period of temperature oscillations is several hundred years, the forest tree community should adjust to these fluctuations both by changing genotype frequency and by selectively increasing the size of certain populations. This hypothesis is supported by the following calculations. For seasonal selection to occur, generation time (T_G) should not exceed 2–3 weeks, and relative birth rate should be such as to ensure the conversion of a rare genotype into a dominant one over a period not longer than 1–2 months. All microorganisms and some small invertebrates meet these criteria (Gurevičiūtė et al., 1989), while temperate trees do not, as their generation

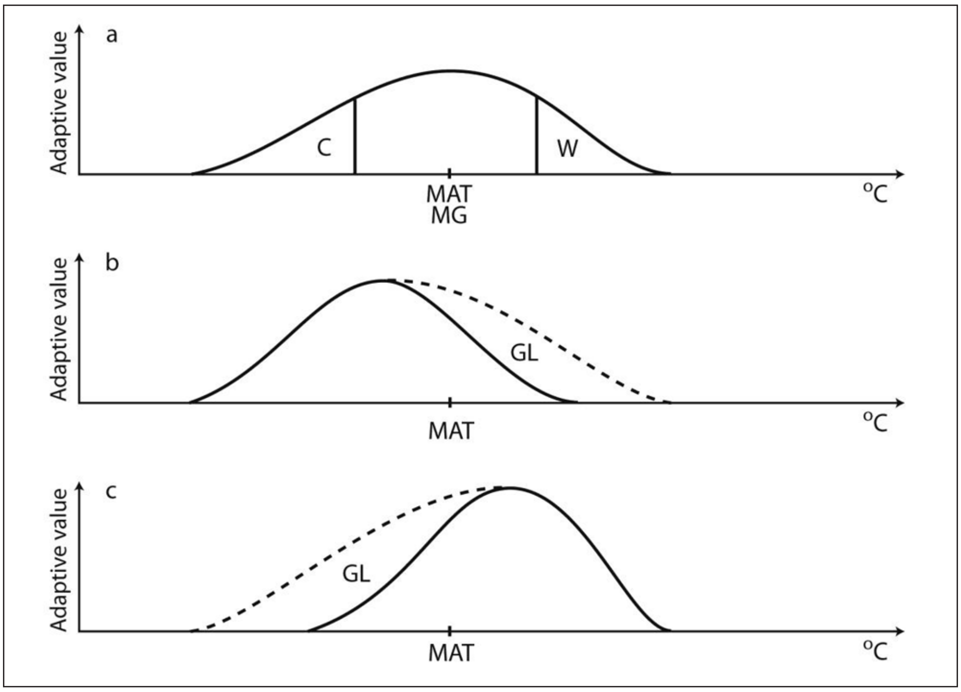

Fig. 3. Hypothetical year-to-year selection in young tree cohorts. Adaptive value here can be measured as the establishment probability of seedlings. Panel *a* shows the structure of a yearly seed cohort; panel *b*, the structure of the established seedling cohort in cold years; panel *c*, the structure of the established seedling cohort in warm years. *MAT* – mean annual temperature; *MG* – mean genotype; *C* – cold year genotypes; *W* – warm year genotypes. *GL* – genetic load or maladapted genotypes

time is often within the range of 20–50 years (Larcher, 2003) which exceeds that of small animals (T_G = 1–2 weeks) more than 1,000-fold. Therefore, heterogeneous populations of trees should easily adjust to oscillations with periods over 1,000 years: when the climate is warming, the frequency of heat-preferring genotypes should increase, whereas cold climate periods should lead to dominance of cold-preferring genotypes. Although a delay in the response is as unavoidable as in the case of seasonal selection, the positive effect of such changes is clear. Such a type of selection could be called multi-year selection. Just like seasonal selection, however, it is unlikely to have long-term evolutionary consequences, because in this case frequencies of pre-adapted genotypes would merely fluctuate around certain means, those of the climate itself. This period of time would also be long enough for populations of some species to grow at the expense of others. The rate of the species sorting process is also restricted by generation time and fertility. Thus, in principle, a year in the life of soil microorganisms is equivalent to a millennium in that of a tree community: during a year soil microorganisms manage to make full use of the same three adaptation modes (Fig. 2) as a tree community over a millennium. This analogy was pointed out by Padisak (1994) for plankton succession: "On the scale of generation times, periods of several months in plankton succession correspond to decades in grassland and centuries in forest succession [...]. In this way, the "plankton year" is analogous to glacial and interglacial cycles."

ARE TEMPERATE FORESTS PRE-ADAPTED TO CURRENT CLIMATE CHANGE?

What about genotypes and species pre-adapted to the projected climate warming? Researchers' opinions on this issue are divided: many of them (e. g. Davis, Shaw, 2001; Rehfeldt et al., 2002) are inclined to believe that genes and genotypes pre-adapted to new prospective environmental conditions can hardly be stored in the existing gene pools. More importantly, the traditional Darwinian logic seems to contradict this hypothesis. Others (Kelly et al., 2003) claim that the process of adaptation will be successful due to “warm-year” genotypes which already exist in most tree populations: their frequency will increase, while that of “cold-year” genotypes will, on the contrary, decrease. Such a viewpoint, however, may be somewhat too optimistic, as Kelly and his fellow researchers have in mind genotypes that help populations to adapt to routine year-to-year fluctuations. These year-to-year differences in mean annual temperatures amount to merely 1 °C, or even less, and are not related to the current climate warming altogether.

HAT suggests addressing this problem from a somewhat unusual standpoint. This theory holds (see above) that information on environmental changes previously experienced by populations is stored in their gene pools. A recurrent environmental change induces a retrieval of the stored information on that change which is consequently used as an adaptive response. However, HAT says nothing about how far back the genetic memory goes. Nonetheless, this hypothesis may prove handy at the present research stage where we rely on intuition as a guide rather than on precise data. It is just necessary to clarify whether periods of climate warming similar to the predicted one occurred a few hundred or thousand years ago, as the genetic memory should go that far back, at least in the case of trees. The “plasticity margin” of several °C that is characteristic of temperate forests (Lekevičius et al., 2011) suggests that this climatic zone experienced warmings greater than the one observed presently.

The occurrence of such long-term climate oscillations in the past is beyond doubt. In the northern hemisphere, periods of climate warming similar to the one currently observed or predicted for the first half of this century, have probably occurred in the third decade of the last century (Alley et al., 2003), as well as approximately 1,000 years and 7,000 years ago, not to mention the episode that took place at the beginning of the Holocene, approximately 11,700 years ago (Pielou, 1991; Bradley et al., 2003; Overpeck et al., 2003; Alley et al., 2003; Moberg et al., 2005). Pielou (1991) detected a 2,500 year-long periodicity in recurrent climatic oscillations during the last 20,000 years. With this periodicity, even populations of oaks and firs ($T_G \approx 70–80$ years; Larcher, 2003) should be able to adjust the frequency of heat- and cold-preferring genotypes without difficulty provided such genotypes exist. Unfortunately, it seems there are no data on how frequencies of any genotypes in local plant populations have changed over that period.

Some of these warming periods were not weaker than the one forecasted for the first half of the 21st century, i. e. an increase in air temperature of 1–2 °C in comparison with the end of the 20th century. In the historical period climate has been changing unceasingly within rather wide limits, and sometimes even faster than predicted for this century (Alley et al., 2003). Many of the trees that experienced the warming of the third decade of the 20th century are still alive today. Just a few of those that experienced the warming of the Middle Ages have survived to this day, but a great number of their 2nd- or 3rd-generation progeny should be present in forests. We are separated from the pronounced warming that ended approximately 5,000 years ago by 10–100 tree generations, a reasonably small number from the standpoint of population genetics.

One of the possibilities to adapt is successful reactivation of silenced genes or “lost” development programs (Marshall et al., 1994; Mattick, 2004; Schlichting, 2008). These genes are sometimes called pseudogenes or genomic fossils, and the choice of such names seems to be grounded: these genes may preserve the potency of being activated for thousands, and sometimes millions of years (Marshall et al., 1994). It is hard to reject the idea that among the billions of seeds and seedlings that germinate every year and are discarded as genetic load by selection in current temperate forests, there may be some types that will become “wild” and spread in populations during the next decades.

Therefore it is quite probable that forest tree communities today still store information on climatic oscillations that have occurred over the last 10–20 thousand years in the form of pre-adapted, if rare, species, genotypes, and genes. If global warming continues unabated for a long time, however, we might enter a period in which environmental conditions have no analogue in the past and, hence, in which there are not enough structures pre-adapted to them. As a result, forest ecosystems might collapse and undergo major long-term reorganizations.

Another possibility is adaptation of plants *in situ* due to gene flow from lower latitudes, especially through pollen migration. The possibility of replenishing gene pools of populations growing under high latitudes with heat-preferring genes from lower latitudes seems realistic although this would take centuries (Lindgren et al., 1995; Davis, Shaw, 2001; Rehfeldt et al., 2002; Hamrick, 2004; Siljamo et al., 2008; Kremer et al., 2012). The existing records show that pollen of wind-pollinated trees travel hundreds of kilometres over a short period of time. Inflowing genes that were rejected by selection just a few decades ago might soon gain supremacy over indigenous ones and be promoted by selection.

According to HAT, life is not a superorganism as it is contradictory in its deep nature (Lekevičius, 1986). Biotic attraction (cooperation and mutualism) and biotic repulsion (competition and exploitative relations) are in a dynamic equilibrium, and this feature is characteristic of all organizational levels. Therefore adaptation – even adaptation to recurrent environmental conditions – does not preclude the possibility of destabilizing behaviours at different levels of organization. As has been mentioned above, adaptive rearrangements take time. Physiological rearrangements may last hours, days or even weeks. A change in gene frequency may take some weeks or months in the case of small organisms, and many years in the case of large organisms such as trees. Similar period of time is needed for populations to increase in abundance. In such circumstances it is difficult to expect the prolonged existence of undisturbed equilibrium between communities and their abiotic environment even in the case of periodical (diurnal, seasonal, year-to-year and multi-year) fluctuations within usual limits. For example, during seasonal selection warmth-adapted genotypes begin to dominate in a daphnid population no earlier than 1–1.5 months after the sun warms the water (Gurevičiūtė et al., 1989). Thus, some disequilibrium is unavoidable. Similarly, some European trees probably have not yet reached equilibrium with the modern climate and soil due to slow migration rates (the postglacial migrational lag hypothesis; Svening et al., 2008).

Such equilibrium should be possible presumably only when organisms are equipped with intrinsic "clocks", i. e. when adaptive reactions are automatic and do not need any environmental cue. It is well known that endogenous circadian and circannual rhythms are characteristic of many species, and their adaptive role is also well known (e. g. Johnsson, 2008). But these "clocks" are usually the features of individual adaptive mechanisms, not populational and biocenotic ones.

So, in natural conditions, the suboptimal environment presumably should be much more frequent than optimal, especially in temperate climate. Additional difficulties for adaptation may arise when the environment is changing in a random manner. For example, unusual heat waves are the most likely outcomes of current climate warming. The primary production of temperate forests and their nutrient cycles are likely to suffer damage only in a case when air temperature reaches approximately the same limit, i. e. about 40 °C (Lekevičius et al., 2011). Despite this, elimination of some genotypes is possible even below this temperature.

HAT predicts the existence of a large number of complementary functional analogues, i. e. structures that can perform analogous functions with respect to their biotic environment but whose abiotic optima do not coincide. Accordingly, two "attraction centres" should emerge when ecosystems adapt to changes in abiotic conditions: the first one is the abiotic factor itself, which demands resistance to it, and the second one is the biotic environment, which demands co-adaptation. When the past abiotic conditions recur, the same set of co-adapted genes, genotypes and species are favoured and (in an ideal situation) the antagonism within it is precluded. The point where trajectories of community dynamics converge is generally unique because at this point individuals and species are not only adapted, but also co-adapted. But this does not mean that co-adaptation should be preserved in all cases. Each individual and each species responds to abiotic changes individually, and their reaction norms, generation times and fertility may differ greatly. So, mismatches between previously co-adapted individuals and species become possible, as seems to be the case with current climate warming (Parmesan, 2006; van der Putten et al., 2010). If climate warming does proceed at unprecedented rates as compared with the historical records, as some authors argue (Jones, Mann, 2004), such mismatches are to be expected.

CONCLUDING REMARKS

Adaptation is a multifarious and complex process that is still relatively poorly known under natural conditions. Better known are probably biochemical and physiological processes, the study of which has deep-rooted traditions dating back to at least 19th century. As investigations of other mechanisms have started more recently, our comprehension of these mechanisms and of their interdependence is rather limited. Nevertheless, a general ecosystems plasticity theory should be feasible. The aim of our article was to show that this is indeed the case, and that such a theory provides important insights into the responses of temperate forests to environmental changes. We showed that a variety of adaptation mechanisms are at the disposal of natural forest communities, that these mechanisms are integrated into a nested hierarchy, and that in real-life situations they often operate simultaneously, each of them contributing to the plasticity of individuals, populations and communities in a specific way. The theory we have presented does not predict sensitivity thresholds beyond which a specific adaptation mechanism is triggered off. On the other hand, any adaptation is an energy- and time-consuming process. All forest organisms are involved in the endless process of adaptation to their environment, because before the adaptation process to a routine environmental change is completed, another one takes place, and proceeds *ad infinitum*. Life on Earth is dynamic, ever-changing and ever-adapting, because its environment is extremely variable, both temporally and spatially. Therefore, it is doubtful that life can ever achieve a true equilibrium with its environment. Biological and ecological systems are fundamentally non-equilibrium systems, in which equilibria are but a convenient simplification for specific processes at specific scales.

We believe that the material presented in this paper demonstrates some of the advantages of the hierarchical approach to complex biological and ecological systems (Allen, Starr, 1982; Salthe, 1985; O'Neill et al., 1986). Although the idea that all phenomena in animate nature are interdependent is by no means new, few biologists or ecologists employ it as a guiding principle in their practical work, which consequently negatively affects its quality (Krebs, 2006). Some researchers focus only on individual adaptation mechanisms, others on the maintenance of polymorphism and fluctuations in the frequency of pre-adapted genotypes, still others on ecological successions induced by environmental impacts or on evolutionary responses to global changes. To see the overall picture, one has to put on special panoramic theoretical glasses. Of course, the panoramic view shows up at the cost of some details. But missing the panorama is more detrimental than missing a detail. By focusing only on details, each of us risks overloading his or her research field with a mass of unrelated facts that lose their broader meaning.

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MIŠKO EKOSISTEMŲ ADAPTYVUMAS IR FUNKCINIS STABILUMAS: KONCEPTUALUS HIERARCHINIS POŽIŪRIS

Santrauka

Šiame straipsnyje mes pristatome konceptualų hierarchinį požiūrį į miško ekosistemų bei populiacijų adaptyvumą ir funkcinį stabilumą besikaitaliojančių aplinkos sąlygų fone, ypač akcentuodami vidutinio klimato medžius. Gamtinėms ekosistemoms yra būdingos tam tikros adaptyvios reakcijos į aplinkos pokyčius, tarp jų – diferencinis genų aktyvumas ir fenotipinis plastiškumas (individualūs mechanizmai), diferencinė genotipų reprodukcija (populiaciniai mechanizmai) ir populiacijų dydžio pokyčiai (biocenotiniai mechanizmai). Mes tiriame, kurie iš šių atsakų į besikaitaliojančią aplinką yra matomi vidutinio klimato miškuose. Sekdami hierarchine adaptyvumo teorija mes traktuojame prisitaikymą kaip niekada nepasibaigiantį daugialygį hierarchinį procesą, kurio metu individai, populiacijos ir bendrijos prisiderina prie aplinkos pokyčių. Šių prisiderinimų dėka stabilizuojami visos ekosistemos rodikliai, tokie kaip pirminė produkcija ir medžiagų ciklas. Mes teigiame, kad miško medžiams ir dirvos mikroorganizmams yra būdingos apytiksliai tokios pat plastiškumo ribos, o adaptyvių persitvarkymų greitis abiem atvejais yra skirtingas. Mes manome, kad vieneri mikroorganizmų metai prilygsta medžių tūkstantmečiui, todėl miško medžių bendrijos turėtų prisiderinti prie daugiamečių klimato svyravimų taip pat lengvai, kaip mikroorganizmai prisitaiko prie sezoninių pokyčių. Toks prisiderinimas yra galimas preadaptuotų genų, genotipų ir rūšių suaktyvėjimo ar plitimo dėka.

Raktažodžiai: hierarchinė adaptyvumo teorija, plastiškumas, genotipų įvairovė, rūšių įvairovė, klimato kaita