

Review

Concept for Genetic Monitoring of Hemiboreal Tree Dynamics in Lithuania

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Abstract: In this review, we focus on the importance of the dynamics of hemiboreal trees in the existing forest landscape and habitats for the genetic monitoring of community phenology, in order to obtain characteristic plant cycles as well as their responses to seasonal and climatic changes. The goal of our review is to: (i) determine the regenerative behaviour of hemiboreal tree species, (ii) propose a concept for the genetic monitoring of tree dynamics in the main forest habitat types of Lithuania's forest landscape based on field observations, e.g., community phenology, and (iii) discuss ways of forest self-regulation, natural regeneration, and reproduction. We have chosen Lithuania as a case study for this review because it is a Northern European country that falls completely within the hemiboreal forest zone, which is often overlooked in terms of climate change effects. Our review highlights the importance of understanding the genetic responses of individual tree species and how they interact in the forest community after disturbance, as well as the need to sustainably monitor them at habitat and landscape scales. To enhance the adaptive potential and associated ecosystem services of forests, we propose the development of landscape-genetic monitoring of the differential dynamic properties of ecosystems.

Keywords: tree species; natural regeneration; community phenology; forest landscape; habitat types



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1. Introduction

Observed climate change (CC) has already led to a wide range of impacts on environmental systems, forests, economies, and human health in Europe. These impacts vary across main biogeographical regions in Europe depending on climatic, geographic, and socio-economic conditions. In northern Europe's forest ecosystems, temperature rises larger than the European average increase the risk of damage from winter storms and heavy precipitation events, and hotter summers affect tree growth and resistance to pests and diseases [1–4]. In the light of CC, the resilience of species and forest ecosystems depends on the extent and structure of phenotypic plasticity, genetic variation, and adaptive potential, as well as dispersal ability [5,6]. Different species face different risks due to CC since their responses to climate in terms of community phenology and stress resistance as well as their dispersal rates differ [7–9]. For this reason, conservation of forest ecosystems, sustainable use of forest resources (and forest genetic resources (FGR)), and sustainable forest management (SFM) are the main goals of monitoring programmes in forest ecosystems at the national and international levels [10–17]. Furthermore, dynamic conservation of FGR underlines the importance of the maintenance of evolutionary and adaptive processes in tree populations to ensure ongoing constant adaptation [18,19]. Therefore, multispecies landscape-genetic or landscape-genomic surveillance is a promising approach in achieving successful conservation strategies as it is almost impossible to deduce general landscape effects on gene flow or local adaptation from single-species studies [20].

Forests are characterized by the development of contiguous communities of trees sufficiently uniform in composition, structure, age, size, class, distribution, spatial arrangement,

site quality, condition, or location to distinguish them from adjacent communities created by human intervention [21–23]. It is generally acknowledged that naturally dynamic forests are more resilient to CC and disturbances compared to single species plantations [21]. This is because the life history traits and strategies of individual species are intrinsically related to forest disturbances and site conditions and account for the interactions among the patterns of species distribution [24,25]. Moreover, the severity and frequency of disturbances along with the environmental characteristics affect how forests develop through general physiognomic stages: stand initiation, stem exclusion, understorey re-initiation, and old growth [26]. Following large-scale but short-term disturbances, such as large windstorms or fire, reforestation in the hemiboreal zone is rapid, where species regenerate by re-sprouting or from wind- and water-dispersed seeds. However, following longer-term disturbances such as repeated logging and conversion to short-rotation monoculture plantation forestry, reforestation towards a natural forest ecosystem may take two or more centuries as succession begins with early-successional herb, shrub, and tree species, and finalizes with late-successional species. Thus, monitoring and understanding regeneration processes of forest ecosystems following a disturbance requires knowledge of the genetic responses from individual tree species and how they interact within the local forest community [27–29]. This is crucial for attaining SFM for both conservation and wood production.

Human impact on tree species occurs directly through population transfer, regeneration, and the silvicultural regimes applied, and this impact is large as it lasts for centuries [30,31]. However, it will be many years before tree-breeding programmes for all important tropical and north temperate tree species will result in the conservation of gene resources in clone banks and seed orchards, and in the production of commercial quantities of seed of the correct provenance [32]. In the meantime, the elimination of the world's remaining natural forest ecosystems continues, and evolutionary centres, sources of great genetic variability and new forms of plant life, are being massively disrupted or destroyed [33]. Wood harvesting has a direct impact on the genetic diversity of tree populations through changes in population size (effective population size), age and size distribution, density, spatial distribution of trees and genotypes, etc. Non-commercial forest species are also affected by logging, as it causes alterations in environmental conditions for animals and plants [34]. In order to fully understand how management systems affect the sustainable use of forests and their conservation in the long term, forest genetic monitoring (FGM) can serve as an appropriate tool [10]. Konnert et al. [35] confirmed the necessity and urgency for developing an FGM system, as problems in the genetic processes of tree populations are usually not immediately observable (e.g., Piotti et al. [36], Hoban et al. [37]) by measuring the natural regeneration or vitality of seeds. However, for an effective genetic monitoring programme with respect to the detection of management impact, it is first necessary to assess the baseline data, i.e., the random fluctuations of the genetic structure of natural populations, in order to be able to detect genetic changes caused by anthropogenic factors later on [38].

In the context of CC, the adaptive potential of forests lies in the sustainable management and monitoring of natural regeneration and reproduction to ensure that the physical and biological conditions of forest ecosystems self-regulate to support natural selection and native biodiversity. It can be concluded that genetic studies at the level of forest regeneration dynamics of trees are necessary [39,40]. The goal of our review is to: (i) determine the regenerative behaviour of hemiboreal tree species, (ii) propose a concept for the genetic monitoring of tree dynamics in the main forest habitat types of Lithuania's forest landscape, and (iii) discuss ways of forest self-regulation, natural regeneration, and reproduction.

2. Genetic Processes of Tree Populations

2.1. Genetic Structure of Tree Species

The traits of hemiboreal trees' life history are a manifestation of species patterns and processes recurring over the scales of species distributions [41,42]. There are contrasting regeneration patterns of early-successional trees or large gap fillers that have a stem growth

type developed to maximize their structural profile, whereas late-successional or small gap makers exhibit a crown growth type that allows them to outcompete their competitors to regenerate in advance under shade [43,44]. Early-successional plant species, or the insects that feed on them, are almost by definition excellent dispersers [45]. However, the distinction between early-successional and late-successional species is subjective; there is no magical moment when a forest stops undergoing succession, and the probability of germination, growth, and recruitment depends on a species genetic profile and life history traits to deal with a variety of environmental characteristics [29,46,47]. Whenever the environment deviates from the optimum, genotypic fitness of a species ensures that biotic processes can compensate for disadvantageous changes [48]. In other words, the variety of the life history of a species and how it interacts in the community is a manifestation of a genetic code written in the genomes of species, which exist for time intervals of the order of several million years—the average lifespan of a species [42]. The past interaction of evolutionary factors—mutation, genetic drift, natural selection, gene flow, and phenotypic plasticity—is responsible for the standing population's genetic structure and variation both within and between species [30]. Mutation is the engine of evolution in that it generates the genetic variation on which natural selection acts, therefore the inclusion of genetic information from multiple species is critical because even functionally similar species can be characterized by very different evolutionary histories and contemporary genetic patterns that can play a major role in providing resilience to future change [49,50].

Long-lived trees as the foundation species of forest ecosystems provide a matrix of resources and habitats for associated organisms, with interactions ranging from beneficial to detrimental [51]. Length of reproductive age and a long-lasting ability to reproduce sexually or vegetatively help tree species to maintain their genetic structure unchanged after founder population establishment, unless human activity is intensive [30]. The fitness of a genotype refers to the average contribution that carriers of that genotype make to the gene pool of successive generations [52]. Population adaptedness of successive generations describes the ability of a species to live, adapt and reproduce in a wide variety of reproductive environments [52,53]. Reproductive environments of species could be considered as a factor increasing the adaptedness of species, especially under marginal conditions [54]. For instance, if a newly established population is small and has no further contact with leading edge/main distribution (no gene flow), then it can suffer due to low genetic variation, which might lead to genetic drift, high inbreeding, and decline [55–57]. Depending on human activity, e.g., assisted migration, can improve the level of genetic diversity, e.g., through artificial or supplementary planting [58–60].

2.2. Genetic Monitoring System

The aim of FGM is: (1) to assess the current status of FGR and quantify relevant changes in the light of preserving the long-term adaptive evolutionary potential of a species [61]; (2) to provide a practical framework for identifying adaptive evolutionary responses to environmental change [62]; and (3) to observe the dynamics of transition from the present to the future genetic status of a forest stand [35]. The FGM system [61] includes three indicators (natural selection, genetic drift, and a gene flow mating system) which are evaluated based on three demographic verifiers (age and size class distribution, reproductive fitness, and regeneration abundance) and four genetic verifiers (effective population size, allelic richness, latent genetic potential and outcrossing or actual inbreeding rate) [11,63,64]. Genetic monitoring can be used for obtaining early warning signs and guiding conservation, for instance by identifying vulnerable populations [65]. Species distribution modelling [66] is another tool to identify populations that may be candidates for genetic monitoring and conservation. Species at the rear edge of their distribution will be the first ones facing CC impacts and will show the first signs of adaptedness or decline, which would be the earliest signals in the frame of FGM. Finally, the effective population sizes should remain high enough to counteract the decline in population fitness and to retain evolutionary potential for reproductive fitness [64,67]. According to Hoban et al. [68]

the effective population size under which the population has a reduced ability to adapt to environmental change is 500 reproducing trees.

No perfect method is available for assessing the geographical distribution of adaptive diversity within tree species at the European scale [65]. Pan-European climatic zoning as a proxy for the core network for sampling the adaptive diversity found in the genetic conservation units across the continent is useful for practical reasons. The goal of genetic monitoring is to verify the long-term adaptive evolutionary potential of monitored genetic conservation units (GCUs). Thus, the European Forest Genetic Resources Programme (EUFORGEN) working group on genetic monitoring proposed a series of steps to select putative GCUs within the delineated genetic monitoring regions for key tree species [63]. For the precise identification of a GCU, the following additional criteria have been proposed: a population size of at least 50 reproducing trees and at least 4 ha for stand-forming species. In this way, the design and the minimum number of trees allow collecting the basic information necessary to track the dynamics of the stand, for example, reproduction and regeneration processes [63].

2.3. Monitoring of Reproductive Behaviour as a Part of Successful Natural Regeneration

FGM should function on a solid research and observational system containing a set of parameters that provide a certain amount of information about the adaptive-evolutionary potential in natural tree populations [34,61,64,69–71]. Among the three main indicators of FGM (natural selection, genetic variation, and gene flow/mating system), natural selection is one of the most important evolutionary factors that can directly affect and change the allele frequencies of even a small forest population/cohort over a short time and can increase the rate of adaptation to environmental conditions [64]. It is based on the assessment of several verifiers through field observations of seasonal phenomena, such as the abundance and synchrony of flowering, the periodicity and intensity of fructification, the abundance of natural regeneration, etc. In most plant species, the timing of seasonal events—regenerative and reproductive phenophases—can be very sensitive to climate and environmental changes, making phenology one of the most variable characteristics of plants [7,8,72,73]. Nonetheless, the genetic monitoring of community phenology, in order to obtain characteristic plant cycles as well as their responses to seasonal and climatic changes, is a promising tool for conservation and management of GCUs.

Flowering is a key factor influencing reproductive fitness, via gene exchange among genotypes, which determines the genetic variation in the resulting seed crop and the survival success of seedlings and natural regeneration [73]. Two forces affecting genetic variation are genetic drift (which decreases genetic variation within but increases genetic differentiation between local populations) and gene flow (which increases variation within but decreases differentiation between local populations) [74]. The timing of flowering is of key importance for forest tree species as it directly affects gene flow at pollination. Significant changes in the time and synchrony of flowering might alter the structure of plant communities and gene flow between populations [75]. The success of flowering is directly determined by flowering synchrony (i.e., the maturation of female and male flowers at the same time), which is highly sensitive to climate change, so warmer and drier climates can disrupt flowering synchrony and affect genetic variation in seed crops/upcoming generations [73]. Disruption of synchronization between female flower receptivity and pollen shedding can adversely affect panmictic equilibrium [76,77], which can lead to non-random cross-fertilization, increased selfing, a higher percentage of empty seeds, and impaired fructification and natural regeneration [78]. Meteorological conditions, such as mean annual temperature and precipitation, are important factors affecting the intensity and synchrony of flowering [79–81]. In addition to meteorological conditions, the variation and amount of flowering directly depend on resource allocation [73,80,82].

Fructification is the regular production of large seed crops, referred to in forestry as the mast year [64]. According to Merriam-Webster [83], the term “fructification” usually refers to the reproductive organs or cones of a plant, which are a major factor in the transmission of

parental genetic information to offspring. The intensity of fructification and the periodicity between mast years is species-specific and varies with resource accessibility, weather conditions, and genetic control (see Mund et al. [84] and references therein). Consequently, the occurrence and periodicity of the mast year is not the same for tree species and differs in the yield of seed crops. An important point is that trees of the same species often synchronize their reproduction over a larger area, a result of genetic and environmental interaction [85,86]. In addition, the beginning of fructification is also an important sign that indicates the maturation of the tree and shows that a part of the resources is allocated for reproduction [87]. Nonetheless, the mast year cannot guarantee successful germination and the establishment of new natural regeneration, while CC-related stress may adversely affect germination and result in a lack of natural regeneration [88–90].

The full chain of processes from flowering to fructification up to seed germination and the formation of a new forest generation under changing environmental conditions affects the adaptive capacity, distribution and abundance of natural regeneration and species in general. A change in the abundance of natural regeneration in a particular forest stand may indicate an ongoing selection process which has led to the reduction, absence or dieback of seedlings and saplings [64]. If the abundance of natural regeneration is insufficient or if the number of reproducing trees has been reduced, urgent forest management interventions might be required to improve the state of the stand [91]. Thus, the assessment of reproductive fitness within the framework of genetic monitoring indicates the ability of an individual to survive and reproduce and can be assessed as a signal of adaptation to current environmental changes [61,63,64,70]. However, indicator “selection” with its phenology verifiers (flowering, fructification, etc.) and natural regeneration assessment can provide a first insight into the status and dynamics of a forest stand and warn us if it is facing decline. Apart from that, it can be easily implemented as a routine procedure in state forestry and can be carried out by a specialist working in the State Forest Service or in the State Forest Enterprises after some training [64]. In addition, monitoring the phenological behaviour of individual populations is less expensive than genetic analysis; nevertheless, monitoring this indicator alone may not explain the primary causes of change/decline [64]. Therefore, two other indicators of FGM, i.e., genetic variation and gene flow/mating system, may need further monitoring and analysis.

2.4. Genetic Effects of Forest Disturbances

Different disturbances can be remarkably contrasting in terms of biological legacies, and this influences the resulting physical and biological conditions of hemiboreal forests, constantly re-evolving and persisting over millions of years [92,93]. Disturbance regimes are characterized by the type, magnitude and duration of environmental variation, as well as community species tolerance and tree regeneration characteristics [43,94–96]. There is growing evidence that the intrinsic influences of disturbance susceptibility are phylogenetically inherited, implying that species-level traits are constrained by developmental, genetic, or other correlated limitations [97]. For example, ‘functional traits reflecting interspecific variation in reproductive capacity are typically correlated with suites of plant traits representing life history strategies’ [98]. A detailed understanding of past disturbance dynamics and their relationship to human impact and management practices is essential for monitoring forest ecosystems in the light of predicted CC [10]. By itself, detailed understanding is achieved only through FGM that will capitalize on the knowledge regarding existing forest management practices and their impact on genetic diversity. There are a few important points to be aware of: FGM should be applied first to natural tree populations that have been least affected by human activities whenever possible. In this manner we will gather our baseline data as a starting point for genetic monitoring. What is more, we will be able to detect actual human/management impacts on genetic diversity when similar plots with regular forest management are monitored simultaneously. Finally, the main challenge in genetic monitoring under changing environmental conditions, if regular forest

management is carried out on the site, is to identify and differentiate changes caused by humans, not by CC, and vice versa.

The impact of forest management on the genetic processes of long-lived forest ecosystems depends on numerous factors such as the management system applied, stand structure, species biology and ecology, distribution, site-specific conditions and demography [99]. Many productive forests have stand properties that are decisively shaped by past management decisions, such as tree species composition, age distribution, rotation period, and stand structure [25]. Forest management may influence the genetic composition of stands directly through the crop tree selection, different silvicultural systems, breeding, and seed transfer, and indirectly through changes in environmental conditions [10,100]. Wernsdörfer et al. [101] modelled the impact of selective cutting on genetic factors (e.g., genetic diversity, selfing, number and location of fathers (pollinators), mating success, population size versus genetic diversity, etc.) and demography (juvenile mortality) in tropical forests. They concluded that forest management should primarily consider the natural regeneration capabilities of tree species. In Europe natural regeneration by the uniform shelterwood system is still generally preferred for *Fagus sylvatica* and its main associates, such as *Fraxinus excelsior*, *Acer pseudoplatanus*, *Prunus avium*, and *Picea abies* [32,102]. The slow natural regeneration in small patches—the shelterwood system—seems to allow for unrestricted gene flow and thus for the dynamic conservation of genetic multiplicity [10]. In contrast, the seed-tree regeneration method can negatively influence the genetic diversity, heterozygosity, and multiplicity of the offspring generation if remaining seed-trees have a scattered distribution, if there are no overlaps in flowering time and some seed trees produce less or no seed and do not provide shelter to the emerging natural regeneration. Such conditions can build up genetic drift and loss of genetic variation and rare alleles [31,103,104].

In general, the stand remains stable if the cycles of flowering and fruiting are regular and at a certain point in time natural renewal becomes the basis for the formation of a new generation of trees. The abundance of seedlings/saplings due to natural regeneration and survival is indicative of a selection pressure that directly affects reproductive success [64]. For these reasons, applied forest management actions should promote dynamic genetic processes to favour adaptation and to maintain genetic diversity [91]. The number of reproducing trees should be sufficient to ensure random mating, the production of a sufficient number of seeds, and the abundance of seedlings/saplings. Based on tree species reproduction cycles, if any, the natural regeneration of stands can be postponed for several years, waiting for the mast year [64,91]. Reproductive cycles of forest tree species last two, three years or more, seed productivity varies from year to year, and mast years come irregularly. Thus, depending on the biology of the species, the applied forest management and other factors, it might take from several years to several decades before a new generation of forest trees is effectively established [91]. Thinning is beneficial but should not reduce the number of reproducing trees too much (the effective population size). An important aspect of thinning is to keep early and late flowering and flushing of the trees to ensure the diversity of the remaining trees and to allow pollination throughout the flowering period. Thinning is an effective tool for the forester that promotes tree growth and regeneration, restores forest health, and enhances flowering and fructification by releasing space and water/soil nutrients [10,104,105].

The practice of clear-cutting large areas with massive machinery, though in the short run is economically sound, is biologically inimical to natural regeneration of most species, a number of conifer species being the exception where alternative methods of natural regeneration deal with areas of land as units, rather than with single trees [32,106]. Natural regeneration is only possible if old stands are remaining and allowed to reach seed-bearing ages. One highly effective example is employed in the Douglas fir forests along the Pacific slope of Canada and the western United States. Logging by powerful yarder machines using overhead cables creates wedge-shaped gaps of cleared ground. The surrounding forest is standing for years to provide shelter and seed. Abundant seed is carried by wind on to the cleared land and gives rise, in a few years, to a full crop of seedling firs [106]. After these have reached seed-bearing

age, the areas previously left standing may be removed in their turn. Similar systems using a pattern of strips cut across the forest, or circular plots gradually extended until they meet and coalesce, are employed in France and Germany. Here, a forest canopy gap is created by harvesting a small group of trees. Once regeneration of the preferred tree species has reached an acceptable level, the canopy gap is widened through the removal of more mature trees. This process continues until the original forest has been completely removed, leaving a forest containing ecologically different blocks or age classes of trees [107].

3. Lithuania as a Case Study for Europe's Hemiboreal Forests

Lithuania is a Northern European country that falls completely within the hemiboreal forest zone. For this reason, we fit the main forest habitat types of Lithuania's forest landscape, i.e., (1) mixed broadleaved forests, (2) mixed Norway spruce forests, and (3) Scots pine forests, including the 18 forest site types, to the 13 Natura 2000 forest habitat types of European Community importance [108] (Table 1). The Lithuanian forest moisture and fertility classification is based on soil typological groups and the applied Food and Agriculture Organization (FAO) soil classification system [109,110] (Figure 1).

Table 1. Ecological features of hemiboreal forest in Lithuania.

Forest Habitat Types (NATURA 2000 Codes)	Main Forest Types, i.e., Field Layer-Canopy Dominants	Forest Site Types *	Soil Types **
Mixed broadleaved forests (9020 9080 91F0 91E0)	Aegopodio-Quercetum	Nf, Lf	CM, LV
	Carico-mixtoherbo-Fraxinetum	Lf	CM, LV
	Calamagrostido-Betuletum pubescentis	Uc	GL
	Filipendulo-Alnetum glutinosae	Ud	GL
	Urtico-Alnetum glutinosae	Uf	GL
	Carico-irido-Alnetum glutinosae	Pd	HSs-ph-ef
	Carico-Betuletum pubescentis	Pc	HSs-ph-mf
Mixed Norway spruce forests (9050 9160 9180 9190 9070)	Oxalido-Piceetum	Nc	CM, LV, PL, AB, AR, FL
	Myrtillo-oxalido-Piceetum	Lc	CM, LV, PL, AB, AR
	Hepatico-oxalido-Quercetum	Nc, Nd	CM, LV, PL, AB, AR, FL
	Oxalido-nemoroso-Piceetum	Ld	CM, LV, FL
Scots pine forests (9010 9060 91D0 91T0)	Cladonio-Pinetum	Na	RG, AR
	Vaccinio-Pinetum	Na, Nb	RG, AR, PZ
	Vaccinio-myrtillo-Pinetum	Nb	AR, PZ
	Myrtillo-Pinetum	Lb	AR, PL, PZ
	Myrtillo-sphagno-Pinetum	Ub	GL
	Carico-sphagno-Pinetum	Pb	HSf-s
	Ledo-sphagno-Pinetum	Pa	HSf

* Hydrotope and trophotope codes in Lithuanian: N—normally moist, L—temporarily overmoistured, U—overmoistured, P—peatland, and f—very eutrophic soils, d—eutrophic soils, c—mesotrophic soils, b—oligotrophic soils, a—very oligotrophic soils. ** AB—Albeluvisols, AR—Arenosols, CM—Cambisols, FL—Fluvisols, GL—Gleysols, HSf—Fibric Histosols, HSf-s—Terri-Fibric Histosols, HSs-ph-ef—Eutrophi-Pachiterric Histosols, HSs-ph-mf—Mesotrophi-Pachiterric Histosols, LV—Luvisols, PL—Planasols, PZ—Podzols, RG—Regosols.

The tree species of the Lithuanian hemiboreal forest are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst), silver birch and downy birch (*Betula pendula* Roth and *B. pubescens* Ehrh.), black alder and grey alder (*Alnus glutinosa* L. Gaertn. and *A. incana* L. Moench), Eurasian aspen (*Populus tremula* L.), European ash (*Fraxinus excelsior* L.), English oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.), European white elm and wych elm (*Ulmus laevis* Pall. and *U. glabra* Huds.), and Norway maple (*Acer platanoides* L.); the northern border of European hornbeam (*Carpinus betulus* L.) crosses Lithuania [111]. European beech (*Fagus sylvatica* L.) could expand its range into the Baltics [112]. All stands of European larch (*Larix decidua* Mill.) in Lithuania are artificially planted [113].

Lithuania's hemiboreal forest sites can be classified into three main forest habitat types based on the concept of potential vegetation and soils [24,39,111,114]. Mixed broadleaved

forests possess broad ecological amplitude regarding their substrate and soil preferences. Swamp substrate consisting of mixtures of mineral and organic materials, and deposited peat (partially decomposed organic matter) may also be present. The main tree species of these forests in Lithuania are *Quercus robur*, *Tilia cordata*, *Acer platanoides*, *Fraxinus excelsior*, and *Ulmus glabra*, along with *Alnus incana* and *Alnus glutinosa* (Table 1). Other individual non-dominant tree species can also be found here. Phytosociologically, very different communities can develop depending on site factors [115]. Mixed Norway spruce forests can form climax communities on fresh to moist and base-richer soils, where the moisture and humidity have not caused most of the nutrients to leach out, leaving behind the clays and oxides. These forests in Lithuania usually consist of *Betula pendula*, less commonly *Populus tremula* or *Pinus sylvestris*, and on richer sites *Tilia cordata*, *Acer platanoides* and *Ulmus glabra*. In the herb layer, *Oxalis acetosella* prevails. Scots pine forests grow on highly oligotrophic, strongly acid to base-rich soils, on very shallow and dry substrates to wet and oxygen-poor mires, on mineral and peat wetlands. Within raised bogs, the vegetation shows the effects of a high-water table and is nutrient poor. Lithuanian hemiboreal pine forests, which differ from the typical boreal pine forests especially by well-developed undergrowth, consist of nemoral deciduous woody plants. As a rule, they do not show any specific characteristic species; their species composition often represents a mixture of species from various vegetation formations but can be remarkably similar to that of the boreal pine forests (especially on very base-deficient and wetlands sites).

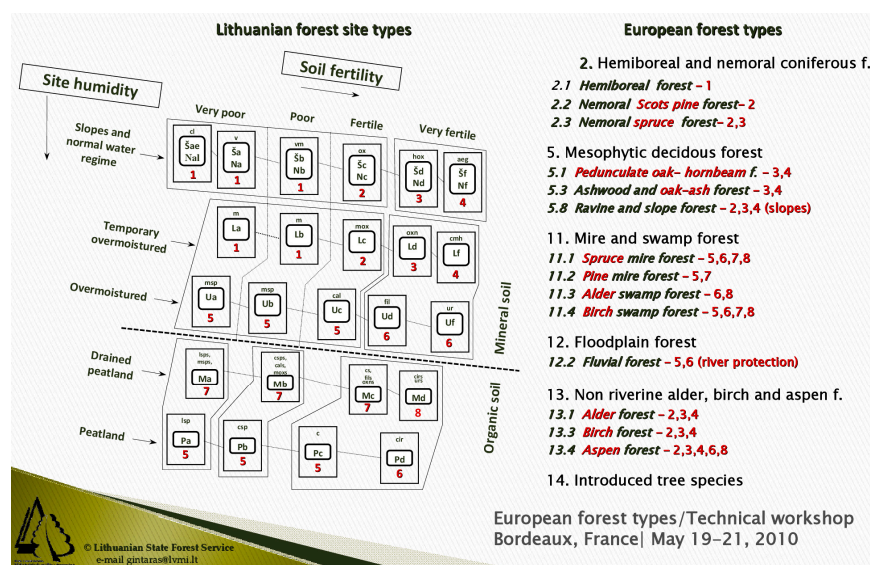


Figure 1. The relationship between Lithuanian forest site types and European forest types [109,111,116,117].

4. Hemiboreal Tree Dynamics of the Main Forest Habitat Types

4.1. Tree Regeneration Strategies in Forest Gaps

Tree species' life histories, generation times, reproductive behaviour, means of dispersal, and other emergent phenomena are connected in a vast and intricate network of self-organizing relationships [118]. The growth dynamics of forest trees are fixed and relatively difficult to modify as a result of physical and biological conditions. In contrast, the seeds of many tree species possess special adaptations that allow them to sit dormant for years waiting for optimal conditions to germinate [32,119]. The strategy of seed storage is widely employed by the trees of hemiboreal forests, and natural regeneration has several advantages over artificial regeneration. One of these advantages is that because the seed sources for natural regeneration are individuals that successfully reproduced in the stand, it is reasonable to expect that they are carriers of the genotype that contributes to the gene pool of successive generations [120]. However, traditional forest management towards maximum sustained yield wood production attempts to control the regeneration processes

of natural forest landscapes [27,121], and thus disrupts the ecological integrity of the long-lived forest ecosystem, which evolves towards continual growth and renewal [122,123].

Morphological, physiological or phenological traits with a demonstrated influence on genotypic fitness in an environmental context typically correlate with suites of regeneration traits and trait trade-offs which differentiate ecological strategies across species [114,124,125]. As the regeneration status of tree species can be used to evaluate whether the development of a forest community is progressing towards the restoration of succession, we classified each hemiboreal forest tree species into one of the four types of tree establishment and growth in forest gaps—the regeneration strategies of tree species [114,124–130]: (i) colonization, (ii) occupation, (iii) invasion, and (iv) expansion (Table 2). Colonization is for species without advance regeneration, and implies that even-aged seedlings are being established and grow only in gaps. Occupation is for species occurring as gap makers; their seeds germinate better in gaps with intermediate canopy openness than in the understorey or large gaps. Invasion implies that trees regenerate from saplings recruited before gap formation; this type is for species occurring as advance regeneration, allowing already established juveniles to survive in newly created gaps. Expansion implies that trees in the forest regenerate as advance regeneration.

Table 2. Tree regeneration strategies: the four types of tree natural establishment and growth in forest gaps [114,124,126] resemble Clark and Clark’s [127] tree species regeneration groups (A–D), Grime’s [128] four main types of secondary strategies in plants (S-R, C-S-R, C-R, and C-S), and Whitmore’s [129] tree species groups (1–4), having increasing “pioneer index”. Modified from Franklin [130].

Growth	Establishment	
	Forest	Gaps
Forest	Expansion (A)—competitive stress-tolerators (C-S): <i>Fagus sylvatica</i> , <i>Tilia cordata</i> . Advanced regeneration under shade and grows best in forest stands; average growth rates, especially as juveniles (1).	Occupation (C)—competitive stress-tolerant ruderals (C-S-R): <i>Fraxinus excelsior</i> , <i>Populus tremula</i> , <i>Quercus robur</i> , <i>Ulmus laevis</i> . Regenerates and grows best in gaps, saplings can survive in closed forests; increased juvenile growth potential over groups A or B (3).
Gaps	Invasion (B)—competitive ruderals (C-R): <i>Acer platanoides</i> , <i>Carpinus betulus</i> , <i>Picea abies</i> , <i>Ulmus glabra</i> . Regenerates in shade but shows heightened association with gaps as saplings; growth rates are as low as group A but increase with size (2).	Colonization (D)—stress-tolerant ruderals (S-R): <i>Alnus glutinosa</i> , <i>Alnus incana</i> , <i>Betula pendula</i> , <i>Betula pubescens</i> , <i>Larix decidua</i> , <i>Pinus sylvestris</i> . Regenerates after gap formation and achieves optimal growth at all juvenile stages; juveniles have the highest growth potential (4).

4.2. Concept of Genetic Monitoring of Hemiboreal Tree Dynamics

Our concept of genetic monitoring of hemiboreal tree dynamics at habitat and landscape scales is based on the dynamic forest habitat types (Table 3), forest type series defined by on-site fertility and moisture content [111,114], environmental specialization of tree species [114], and tree regeneration strategies in forest gaps [114,124,126–130]. It follows the Lithuanian classification of forest types and the layer dominants: forest site type, forest type series (field flora), dominant and secondary tree species. The habitat type aspect in this classification is close to the forest type interpretation in the Russian genetic classification by Kolesnikov [131], while the characteristics of vegetative cover and soils are close to those suggested by Vaičys [109,111] (see forest site types in Table 1). The three dynamic forest habitat types in our concept represent general descriptions of plant community types that reflect the dynamics of vegetation cover that occur in the course of natural

disturbances [39]. In hemiboreal forests, there are three main types of natural disturbance regimes that determine the success of natural regeneration: (1) gap dynamics caused by the death of individual trees or small groups of trees in the absence of fire; (2) successional development after severe stand-replacing disturbances, such as crown fires and large blow-downs (e.g., windthrows, pest outbreaks, etc.); and (3) multi-cohort dynamics related to partial disturbances, such as low-intensity surface fires [43,93,95,96,132,133].

Table 3. Concept of genetic monitoring of hemiboreal tree dynamics in the main forest habitat types of Lithuania’s forest landscape [114,134]. Capital letters X indicate the main tree species that form forest stands, whereas small letters x indicate secondary ones which are a valuable admixture.

Regeneration Strategies of Tree Species: C—Colonization, O—Occupation, I—Invasion, E—Expansion	Dynamic Forest Habitat Types (NATURA 2000 Codes)/Field Layer Codes of the Forest Type Series *																	
	Gap Phase Dynamics with Mixed Broadleaved Forests on Rich Sites (9020 9080 91F0 91E0)						Successional Development in Mixed Norway Spruce Forests on Mesic Sites (9050 9160 9180 9190 9070)						Multi-Cohort Succession in Scots Pine Forests on Poor Sites (9010 9060 91D0 91T0)					
	aeg *	cmh	cal	fil	ur	cir	c	ox	mox	hox	oxn	cl	v	vm	m	msh	csp	lsp
<i>Alnus glutinosa</i>	C	x	X	X	X	X	X					x						
<i>Alnus incana</i>	C	X	x	x	x			x	x	X	X							
<i>Betula pendula</i>	C	x	x	x	x	x		X	X	X	X		x	x	X			
<i>Betula pubescens</i>	C	x	x	X	X	x	x	X								x	X	
<i>Larix decidua</i>	C							X										
<i>Pinus sylvestris</i>	C						x	X	X			X	X	X	X	X	X	X
<i>Fraxinus excelsior</i>	O	X	X		x	x					X							
<i>Populus tremula</i>	O	x	x		x			x	X	x	X				x			
<i>Quercus robur</i>	O	X	x					x		X	x							
<i>Ulmus laevis</i>	O	X	x								x							
<i>Acer platanoides</i>	I	x								x								
<i>Carpinus betulus</i>	I	x								X								
<i>Picea abies</i>	I			x	x			X	X	X	X			x	x	x		
<i>Ulmus glabra</i>	I	X																
<i>Fagus sylvatica</i>	E									X								
<i>Tilia cordata</i>	E	X								X								

* Field layer codes of the main types of forest plant communities, i.e., forest type series (=forest site types): aeg—Aegopodiosa, c—Caricosa, cal—Calamagrostidosa, cir—Carico-iridosa, cl—Cladoniosa, cmh—Carico-mixtoherbosa, csp—Carico-sphagnosa, fil—Filipendulo-mixtoherbosa, hox—Hepatico-oxalidosa, lsp—Ledo-sphagnosa, m—Myrtilliosa, mox—Myrtillo-oxalidosa, msp—Myrtillo-sphagnosa, ox—Oxalidosa, oxn—Oxalido-nemorosa, ur—Urticosa, v—Vacciniosa, vm—Vaccinio-myrtilliosa.

“Species differences in regeneration strategies are an important part of species regeneration niche and contribute critically to their coexistence and community assembly” [135]. The analysis of tree regeneration in the main forest habitat types of Lithuania’s forest landscape shows that hemiboreal tree species can have singular to multiple niche positions (Table 3). For instance, the position of *Ulmus glabra* is restricted to the gap phase dynamics with mixed broadleaved forests on rich sites and with an invasion type of tree natural regeneration. In contrast, the niche position of *Pinus sylvestris* can be categorized as having successional development in mixed Norway spruce forests on mesic sites, multi-cohort succession in Scots pine forests on poor sites, and gap phase dynamics with mixed broadleaved forests on rich sites with a colonization type of tree natural regeneration. Colonization is the most tree species-rich category, while expansion is the least species-rich category. *Pinus sylvestris*, *Populus tremula*, *Betula pendula*, and *Picea abies* are habitat generalists, while *Ulmus glabra* is a habitat specialist.

Based on the principles of EUFORGEN for forest genetic monitoring [63], two environmental zones are identified in Lithuania: cold and moist—EG, and cool and dry—HI. In total, the Lithuanian National Focal Point (NFP) has registered 131 GCUs in the European Information System on Forest Genetic Resources (EUFGIS) database and 11 GCUs within the EUFORGEN core network for the main tree species—*Alnus glutinosa*, *Betula pendula*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Quercus robur*, and *Tilia cordata*. Based on the EUFORGEN recommendations for FGM, it should be applied to the GCUs entered into the EUFGIS database and, as far as possible, matched to the units identified by EUFORGEN [63]. Nevertheless, we suggest that the existing FGM system in Lithuania be expanded to include dynamic forest habitat types and canopy species that form forest stands as dominant or co-dominant trees (see Table 3).

5. Ways of Forest Self-Regulation, Natural Regeneration, and Reproduction

Ecological integrity refers to the state or condition of an ecosystem that displays the biodiversity characteristics of the reference, such as tree species composition and community structure, and is capable of self-sustaining [123]. The self-organizing processes that create naturally regenerating forests and enhance natural regeneration in planted forests create habitat heterogeneity and sustain local biodiversity and biotic interactions [136]. These features confer greater ecosystem resilience in the face of CC and disturbances, and habitat models are currently the only ones able to rapidly provide simulations of thousands of species distributions to assess the impact of CC on biodiversity [7].

To improve the legacy of Lithuania's forest landscape and to maintain the natural variation in self-sustaining forest ecosystems, it is necessary to (i) foster the retention and provision of trees with high genotypic fitness, and (ii) promote forest regeneration that both mimics and facilitates hemiboreal tree dynamics of the main forest habitat types. This requires a conceptualization of genetic monitoring of hemiboreal tree dynamics that incorporates landscape genetic patterns [137]. Strengthening protections for retaining landscape genetic patterns and natural reforestation in the future is critical for supporting the European Union's forest, forest genetic resources, and biodiversity strategies [138–140] as well as maintaining forest landscape legacies through sustainable forest management.

Assessment of the relative stability of tree species composition in combination with the edaphic factors of the site has become a key forestry problem because of global climate change and related disturbances [39,40]. Disturbances in the forest impact the community ecology, including the availability of leaves, flowers and fruits that sustain most food chains in this ecosystem [8]. We think that the impact of changes in the forest ecosystem can be measured indirectly through the effects on community phenology by analysing the dynamics of recovery in a multiscale fashion, from genetic variation via tree regeneration characteristics (e.g., regeneration composition vs. canopy composition) to multipopulation structure via disturbance characteristics (e.g., disturbance regimes vs. management treatments). To enhance the adaptive potential and associated ecosystem services of forests, we propose the development of landscape-genetic monitoring of the differential dynamic properties of ecosystems [20,141].

Assisted natural regeneration of forests after harvesting aims to accelerate, rather than replace, natural successional processes by removing or reducing barriers to regeneration such as soil degradation, competition with weedy species, and recurring disturbances (e.g., fire, grazing and wood harvesting) [123]. It allows the existing forest structure and composition to unfold and the successional process-pattern of cause and effect to emerge. Unfortunately, under current forest management activities, forests do not have the complete range of opportunities for self-regulation and natural forest dynamics to provide the full range of multiple benefits for human well-being and the conservation of native biodiversity. National environmental legislation often does not place enough emphasis on the protection of long-lived forest ecosystems and their development towards self-regulation, natural regeneration, and reproduction.

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