Genetic Monitoring of Hemiboreal Tree Dynamics

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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. 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. 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.

tree species natural regeneration community phenology

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][2][3][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][8][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][11][12][13][14][15][16][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][22][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][28][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].

2. Genetic Processes of Tree Populations

The traits of hemiboreal trees' life history are a manifestation of species patterns and processes recurring over the scales of species distributions [41,42]. 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]. Whenever the environment deviates from the optimum, genotypic fitness of a species ensures that biotic processes can compensate for disadvantageous changes [48]. The fitness of a genotype refers to the average contribution that carriers of that genotype make to the gene pool of successive generations [52]. 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]. 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]. 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]. 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]. 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].

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 genetic conservation units (GCUs).

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, researchers 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 [39]. The Lithuanian forest moisture and fertility classification is based on soil typological groups and the applied Food and Agriculture Organization (FAO) soil classification system [40][41].

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 [42]. European beech (*Fagus sylvatica* L.) could expand its range into the Baltics [43]. All stands of European larch (*Larix decidua* Mill.) in Lithuania are artificially planted [44].

Lithuania’s hemiboreal forest sites can be classified into three main forest habitat types based on the concept of potential vegetation and soils [24][42][45][46]. 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*. Other individual non-dominant tree species can also be found here. Phytosociologically, very different communities can develop depending on site factors [47]. 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).

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 [48]. 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][49]. 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 [50]. However, traditional forest management towards maximum sustained yield wood production attempts to control the regeneration processes of natural forest landscapes [27][51], and thus disrupts the ecological integrity of the long-lived forest ecosystem, which evolves towards continual growth and renewal [52][53].

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 [46][54][55]. 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, researchers 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 [46][54][55][56][57][58][59][60]: (i) colonization, (ii) occupation, (iii) invasion, and (iv) expansion. 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.

4.2. Concept of Genetic Monitoring of Hemiboreal Tree Dynamics

Concept of genetic monitoring of hemiboreal tree dynamics at habitat and landscape scales is based on the dynamic forest habitat types, forest type series defined by on-site fertility and moisture content [42][46], environmental specialization of tree species [46], and tree regeneration strategies in forest gaps [46][54][56][57][58][59][60]. 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 [61], while the characteristics of vegetative cover and soils are close to those suggested by Vaičys [40][42]. The three dynamic forest habitat types in concept represent general descriptions of plant community types that reflect the dynamics of vegetation cover that occur in the course of natural disturbances [45]. 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 blowdowns (e.g., windthrows, pest outbreaks, etc.); and (3) multi-cohort dynamics related to partial disturbances, such as low-intensity surface fires [62][63][64][65][66][67].

“Species differences in regeneration strategies are an important part of species regeneration niche and contribute critically to their coexistence and community assembly” [68]. 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. 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 [69], 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 [69]. Nevertheless, researchers 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.

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 [53]. 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 [70]. 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 [71]. 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 [72][73][74] 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 [45][75]. 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]. Researchers 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, researchers propose the development of landscape-genetic monitoring of the differential dynamic properties of ecosystems [20][76].

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) [53]. 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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