

Hemiboreal Tree Dynamics

Subjects: **Biology**

Contributor: Raimundas Petrokas , Diana-Abasi Ibanga , Michael Manton

Climate change and the associated disturbances have disrupted the relative stability of tree species composition in hemiboreal forests. The natural ecology of forest communities, including species occurrence and composition, forest structure, and food webs, have been affected. Yet, the hemiboreal forest zone of Lithuania is the least studied in the country for climate change risks and possible management adaption techniques. Moreover, the adverse effects of the phenomenon of global climate change can undermine the resilience of forest ecology in terms of its capacity for natural regeneration to occur successfully on the scale of the expected time. Especially since forests are meta-networks that constantly evolve toward the successional processes and patterns that cannot be reached at an individual species level. Therefore, in the context of hemiboreal forests, assisted natural regeneration lays the groundwork necessary to consider the life-cycle features of trees that affect the organic relationships between individual species and ecological communities indirectly via their effects on growth, reproduction, and survival, such as tree regeneration strategies that correspond to the various trade-offs in the adaptations to competition, stress, and forest disturbances. With the concept of assisted natural regeneration, embedded in the principle of deep ecology, the natural powers of forest ecology can be revitalized and fast-tracked to keep up with the pace of global climate change or even overtake it ahead its disruptions.

hemiboreal trees

assisted natural regeneration

deep ecology

1. Introduction

Natural recurring forest processes are often self-organised and implicate sustainability processes in environmental changes. Niche construction, ecological engineering, and biosemiotics processes are different forms of indirect, background interaction and communication of organisms in the environment ^[1]. Self-organisation of an ecosystem includes all the diversity that cannot be reduced to the properties of an individual system's components, such as molecules, genes, populations, and species in both time and space ^[2]. Meaning is generated across all the organisational levels ^[3]. The strategy of life expansion is realized through the spread of life in space—the proliferation and collaborative construction of ecosystems and the biosphere by organisms. Forests are multi-scale, multi-organism networks that constantly evolve toward the successional processes and patterns of natural regeneration. In this direction, the focus is on the super-organism approach of forest communities that considers succession as a comprehensive ecological process of multiple events where the forest vegetation communities are directly related to environmental condition with regard to climate change ^[4].

The life history traits of species are controlled by natural patterns and processes recurring over time and space at multiple scales ^{[5][6]}. Natural selection has matched trees to site and environmental conditions for millennia ^[7] and

is considered a key evolutionary process that can increase the adaptation rate of species to environmental change [8]. Natural selection can be confirmed through field observations of ecological communities and their development towards self-organisation. Tree species' life histories, reproductive character, regeneration times, mode of dispersion, and other evolutionary phenomena are interconnected in the immense and complex system of self-sustaining interactions of forest communities [9]. The ecology of a forest never ceases to evolve. The probability of seed germination, tree growth, development and recruitment is dependent on a species' genetic profiles and life history traits to cope with the changes in environmental conditions [10][11][12]. Dynamics in forest communities are driven by a wide range of factors, including species' invariable life history strategies [4].

However, traditional forest management, climate change and increased disturbances have disrupted the relative stability of tree species composition in combination with the edaphic site conditions in European hemiboreal forests [13][14]. This is a key problem. The natural ecology of forest communities, including species occurrence and composition, forest structure, and food webs have been affected [15]. Developing knowledge about natural forest disturbance dynamics and their relationship to anthropogenic impacts and management practices is essential towards the mitigation of impacts on forest ecosystems in the light of climate change [16]. This warrants the basis for proposing the assisted natural regeneration (ANR) strategy as an alternative adaptive model for forest management in Europe.

The self-organisation of an ecological community can play a major role in providing resilience to future climate change [17][18][19] but must be accelerated with ANR strategies. In forest management, the most fundamental methods of ANR are the protection and promotion of parent tree growth and regeneration specific to site conditions and natural disturbance regimes [20]. This is in line with the philosophy of deep ecology which emphasizes diversity as the bastion of sustainability.

2. European Hemiboreal Tree Species: The Case of Lithuania

Focusing on the European hemiboreal forests of Lithuania because it is one of only two countries (Latvia and Lithuania) that falls completely within the hemiboreal forest zone in Europe [21]. The hemiboreal forest zone is the flux zone between the temperate forest zone to the south and boreal zone to the north. Unfortunately, the forests of the hemiboreal zone are often overlooked in climate impact and adaption studies, while attention is focused on the other two zones [14]. Assisted natural regeneration (ANR) and deep ecology in the context of Lithuanian forest ecosystems are not linked by any previous works. Despite this, ANR is very relevant in the context of hemiboreal Lithuania where there is an increasing need to maintain forest biodiversity, while at the same time enhancing the cultural diversity of Lithuania.

Lithuania's hemiboreal forest site types (as well as the 13 Natura 2000 forest habitat types of European Community) can be classified into three main forest habitat types based on the concept of potential vegetation and soils [14][22][23]: (1) mixed broadleaved forests on rich sites; (2) mixed species forests on mesic sites dominated by Norway spruce; and (3) Scots pine (*Pinus sylvestris*) forests on poor sites. Soil moisture and fertility of Lithuania's forests are considered the main drivers of forest disturbances and succession [21]. As such, Lithuania's forests have

been classified by the Food and Agriculture Organisation (FAO, Rome, Italy) soil classification system [24][25] based on soil typological groups (Figure 1).

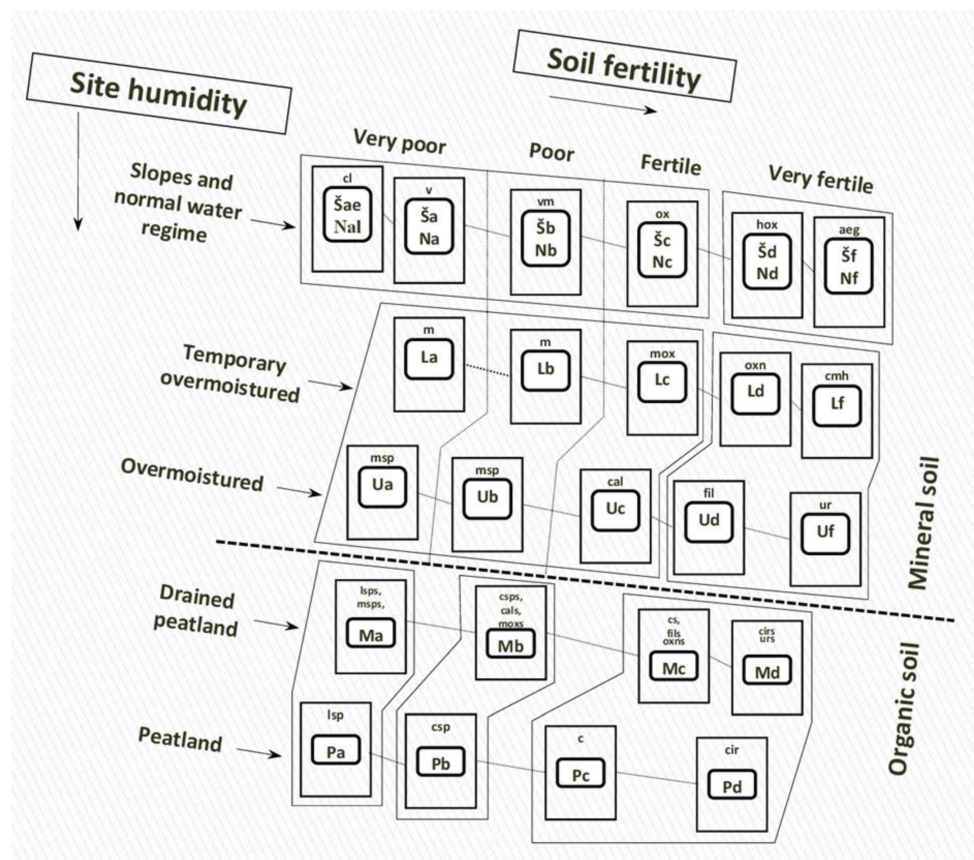


Figure 1. Lithuania's forest site type scheme. The bold codes refer to Lithuania's forest site types based on soil fertility and moisture, and the small non-bold letters refers to the forest vegetation type series [22][24][26]: N—normally moist, L—temporarily over moist, U—over moist, P—peatland, and f—very eutrophic soils, d—eutrophic soils, c—mesotrophic soils, b—oligotrophic soils, a—very oligotrophic soils; 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—*Myrtillosa*, mox—*Myrtillo-oxalidosa*, msp—*Myrtillo-sphagnosa*, ox—*Oxalidosa*, oxn—*Oxalido-nemorosa*, ur—*Urticosa*, v—*Vacciniosa*, vm—*Vaccinio-myrtillosa*.

3. Hemiboreal Tree Dynamics

3.1. Tree Regeneration Strategy

Forests are characterized by the development of contiguous communities of trees that are relatively uniform in composition, structure, age, size, class, distribution, spatial arrangement, site quality, condition, and location to distinguish them from adjacent communities created by human intervention [27][28][29]. The absence of structural legacies at multiple scales is one of the most distinguishing features of modified forests subjected to intense and

frequent anthropogenic disturbances [30][31]. Species' life history traits are interrelated with natural disturbances and associated site conditions, and these account for the interactions (patterns and processes) in species distribution [14][32]. There is also increasing 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 [33]. Being the primary species of forest ecosystems, long-lived trees are pivotal in providing associated organisms with a combination of resources and habitats that range from beneficial to detrimental [34]. Therefore, the forest development and growth dynamics of tree species follow relatively fixed patterns and can be difficult to modify in the light of the interactions of both biological and physical processes. This is also the case with hemiboreal trees' natural regeneration.

There are four tree natural regeneration strategies, i.e., the establishment and growth of trees in forest gaps [35][36][37][38][39]: (i) colonization; (ii) occupation; (iii) invasion; and (iv) expansion (**Table 1**). These are inter-intuitive with Clark and Clark's [40] tree species regeneration groups (A–D), Whitmore's [41] tree species groups, having an increasing “pioneer index” (1–4), and Grime's [42] four types of secondary ecological strategies in trees that are derived from the theoretical triangular scheme of competitor (C), stress-tolerant (S) and ruderal (R) primary plant ecological strategies—stress-tolerant ruderals (S-R), competitive stress-tolerant ruderals (C-S-R), competitive ruderals (C-R), and competitive stress-tolerators (C-S). Colonization (D, 4, S-R) implies that even-aged seedlings are being established after gap formation and grow only in gaps. This relates to stress-tolerant species that possess a ruderal strategy without advanced regeneration. Juveniles have the highest growth potential. A ruderal strategy is a characteristic of many species that never become established in ruderal habitats. Ruderal species are plants that grow only in habitats that have been completely disturbed and damaged by human activity [43]. Occupation (C, 3, C-S-R) relates to the competitive stress-tolerant ruderal strategy species occurring as gap makers. Their seeds germinate better in gaps with intermediate canopy openness than in the understorey or large gaps, saplings can survive in closed forests. Invasion (B, 2, C-R) implies that trees regenerate from saplings recruited before gap or stand formation. This type involves competitive species with a ruderal strategy of advance regeneration, allowing already established juveniles to survive in newly created gaps. Expansion (A, 1, C-S) implies that trees in the forest regenerate as advanced regeneration under shade. This usually involve competitive stress-tolerant species. Juveniles have average growth rates.

Table 1. Conceptual framework of hemiboreal tree dynamics in Lithuania [35][44][45]. Capital letters indicate the main tree species that form forest stands in gap dynamics (G), successional development (S), or multi-cohort succession (M), whereas small letters (g, s, and m) indicate secondary ones which are a valuable admixture in these stands.

| Regeneration Strategy: C—Colonization O—Occupation I—Invasion E—Expansion | | Forest Habitat Types (NATURA 2000 Codes)/Codes of the Lithuanian Forest Type Series * and Forest Site Types ** | | | | | | | | | | | | | | | | | | |
|---|---------------------------|--|----|-----|-----|-----|------|-----------------------------|------|------|-----|-----|-----|-----------------------|----|----|----|------|-----|-----|
| | | Mixed Broadleaved Forests | | | | | | Norway Spruce Mixed Forests | | | | | | Scots Pine Forests | | | | | | |
| | | (9020 9080 91F0 91E0) | | | | | | (9050 9160 9180 9190 9070) | | | | | | (9010 9060 91D0 91T0) | | | | | | |
| | | aeg | * | cmh | cal | Fil | ur | cir | c | ox | mox | hox | oxn | cl | v | vm | m | mspc | csp | lsp |
| | | Nf | Lf | Uc | Ud | Uf | Pd | Pc | Nc | Lc | Nd | Ld | Nal | Na | Nb | Lb | Ub | Pb | Pa | |
| C | <i>Alnus glutinosa</i> | | G | G | G | G | G, S | G, S | | | | G | | | | | | | | |
| C | <i>Alnus incana</i> | G | G | g | G | | | | S, g | S, g | G | G | | | | | | | | |
| C | <i>Betula pendula</i> | G | G | g | G | g | | | S | S | S | S | | s | s | S | | | | |
| C | <i>Betula pubescens</i> | G | G | S | S | g | G | S | | | | | | | | | s | S | | |
| C | <i>Larix decidua</i> | | | | | | | | S | | s | | | | | | | | | |
| C | <i>Pinus sylvestris</i> | | | | | | | S, m | M | M | | | M | M | M | M | M | M | M | |
| O | <i>Fraxinus excelsior</i> | G | G | | G | g | | | | | | G | | | | | | | | |
| O | <i>Populus tremula</i> | G | G | | G | | | | S | S | s | S | | | | S | | | | |
| O | <i>Quercus robur</i> | G | G | | | | | | G | | G | g | | | | | | | | |
| O | <i>Ulmus laevis</i> | G | G | | | | | | | | | g | | | | | | | | |
| I | <i>Acer platanoides</i> | G | | | | | | | | | g | | | | | | | | | |
| I | <i>Carpinus betulus</i> | G | | | | | | | | | G | | | | | | | | | |
| I | <i>Picea abies</i> | | | g | G | | | | S | S | S | S | | s | s | s | | | | |
| I | <i>Ulmus glabra</i> | G | | | | | | | | | | | | | | | | | | |

| Regeneration Strategy: C—Colonization O—Occupation I—Invasion E—Expansion | | Forest Habitat Types (NATURA 2000 Codes)/Codes of the Lithuanian Forest Type Series * and Forest Site Types ** | | | | | | | | | | | | | | | | | | | |
|---|------------------------|--|------------------------------|-----|-----|----|-----|-----------------------------|----|-----|-----|-----|-----|-----------------------|----|--|----------|----|-----|--|--|
| | | Mixed Broadleaved Forests | | | | | | Norway Spruce Mixed Forests | | | | | | Scots Pine Forests | | | | | | | |
| | | (9020 9080 91F0 91E0) | | | | | | (9050 9160 9180 9190 9070) | | | | | | (9010 9060 91D0 91T0) | | | | | | | |
| | | aeg | | | | | | | | | | | | | | | | | | | |
| | | * Nf | cmh | cal | Fil | ur | cir | c | ox | mox | hox | oxn | cl | v | vm | m | mspc | cs | lsp | | |
| | | ** | Lf | Uc | Ud | Uf | Pd | Pc | Nc | Lc | Nd | Ld | Nal | Na | Nb | Lb | Ub | Pb | Pa | | |
| E | <i>Fagus sylvatica</i> | | | | | | | | G | | | G | | | | [13][14][22][23][46][47][48][49][50][51] | | | | | |
| | | | | | | | | | | | | | | | | | [22][52] | | | | |
| E | <i>Tilia cordata</i> | G | [36][37][38][40][41][42][44] | | | | | | | | g | | G | g | | | | | | | |

three dynamic forest habitat types in the conceptual framework represent general descriptions of plant community types that reflect the dynamics of vegetation cover that occur in the course of natural disturbances [13]. In hemiboreal forests, there are three main types of natural disturbance regimes that determine the success of natural selection: (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, large windthrows, pest outbreaks, etc.; and (3) multi-cohort dynamics related to partial disturbances such as low-intensity surface fires [46][47][48][49][50][51]. ** 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. Hemiboreal forests may be legacies of biological and physical disturbances [6][27]. Disturbance regimes are classified by the type, magnitude and duration of environmental variation as well as community (ecosystem) and individual species resilience [47][48][49][53]. Tree species regeneration in hemiboreal zone is generally rapid after large-scale short-term disturbances (e.g., forest fire) but slower after longer term disturbances such as repeated logging or forest conversion to monoculture plantations [44]. Restoration of the original forest ecosystem via natural regeneration can take several centuries as succession begins with early-successional herb, shrub, and tree species, and culminates with late-successional species. In order to understand forest regeneration processes following a disturbance, one needs to be knowledgeable in forest dynamic typology, which can provide a first insight into the status of vegetation cover (i.e., basal, canopy, foliar, or ground cover) and warn that if it is facing decline or an unwanted trajectory. As such, researchers have allocated each hemiboreal tree species to a dominant regeneration strategy that can play an important role in maintaining the resilience of the forest ecology in terms of its ability to regenerate successfully on an expected time scale (Table 1). Therefore, it can be argued that the assisted natural regeneration (ANR) strategy could be a viable means of building hemiboreal forest resilience to cope with future climate change risks.

ANR can be relevant in the context of adaptative management of forest succession and disturbances to sustain tree species and promote forest self-organisation. However, it should be noted here that disturbances are inherently volatile. A forest stand that is subject to a larger-scale disturbance can also be subject to smaller-scale disturbance. For instance, in mixed Norway spruce forest, disturbance can range from a single tree (gap/small patch (G)) to a stand or forest (large patch (S)) sized disturbance (Table 1). Thus, there is no certain rule on

regeneration. Another factor to consider is the type of disturbance. For instance, Scots pine is fire tolerant, and fire stimulates regeneration. Conversely, Norway spruce is fire intolerant and thus is often eliminated together with its seed bank. So, fire creates multi-cohort pine stands and eliminates spruce. Also, the different disturbance regimes of forests undergo generate different age profiles [\[30\]](#).

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