

Lithuanian Forest Tree Successional Categorisation

Subjects: **Plant Sciences**

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Developing forest harvesting regimes that mimic natural forest dynamics requires knowledge on typical species behaviors and how they respond to environmental conditions. Species regeneration and survival after disturbance depends on a species' life history traits. The four types of ecologically invariant life-history trajectories of species turnover are a core component to evaluate if the development of the forest community is progressing towards the restoration of the climatic climax.

life history

species turnover

disturbance generalists

disturbance specialists

succession generalists

succession specialists

climatic climax

forest dynamics

gap colonizers

gap competitors

forest colonizers

forest competitors

1. Introduction

Forests are complex systems of interacting organisms; to manage them for tree species composition and production we need thorough knowledge of the variety of tree species' life histories and how they interact. Within the hemi-boreal forest climatic zone there are three main forest disturbance regimes that host a variety of successional characteristics: (i) stand succession (large or stand replacing disturbance such as severe fire, windthrows, or current clear felling), (ii) cohort dynamics (related to partial disturbances of a stand such as a low intensity ground fire or forest thinning), and (iii) gap dynamics (such as small patch or a fallen tree) ^[1]. Succession is a sequential shift of patterns and processes in terms of the relative abundance of dominant species ^[2]. The succession of forest stands and patches largely determines the extent to which forest communities are able to cope with changes in environmental conditions and forest loss due to natural disturbances or human activity ^{[3][4][5]} ^[6]. Forest disturbances trigger successional events that lead to climatically determined end communities or climatic climax, generally regarded as a position of stability in the development of vegetation ^{[7][8][9]}.

The first definition of climax was described by Clements ^[10] as the ability of species composition to remains stable for more than one tree generation (i.e., the tree species replace themselves) in the absence of disturbance other than tree deaths due to old age. Thus, a forest that can regenerate naturally with the same composition over time can qualify as natural climax. In reality, however, the difference between a successional forest and a climax forest is subjective, as a forest ecosystem is dynamic, where succession is a continual process ^[11]. Although Clements' ^[10] dynamic ecology concept is still valid ^[12], it does not represent the boundless factors impacting ecological

succession. For example, the role and importance of both biotic and abiotic factors in predicting species distributions remains unclear [13][14][15][16][17]. Therefore, no clear conclusion can be drawn as to the successional position of tree species [10]. The probability of species survival and succession after disturbance depends on a species' genetic profile to deal with a variety of environmental characteristics [18]. In other words, a tree's life history traits define its position along its successional pathway that includes functional strategies for reproduction or resource capture [19].

The fundamental principle underlying the theory of invariance is that the laws of nature always have the same form for all observers [20]. This implies that all the elements of any developing living system interact, and thus all elements are ecologically equivalent, as the essence of ecological law and processes lies in invariance by which a living system following a disturbance returns to its stable state [21][22]. From a wildlife perspective, each organism, population, and community have different environmental scales in both time and space [23], and individual species may impact another species' life history traits [24][25]. Thus, there are different perceptions about the interactions among species (that otherwise can survive virtually the same for millions of years), which proceed towards the ecological equivalence of climatically determined end communities [26]. Primary forests exist in a delicate but stable climax with all other components of the ecosystem; not one component can change without compensating changes in the others. For example, harvesting or thinning a forest stand will inevitably be followed by changes in the soil profile, vegetation, and life occurrence [9]. Generally, the dynamics of forest communities can be controlled by a set of ecologically invariant life-history traits of tree species turnovers [9][27][28][29][30]. Therefore, a variety of tree species' life histories and how they are integrated into the forest system need to be summarized as a continuum of ecologically invariant life-history trajectories of species turnover [11].

The natural tendency of forest succession is towards climatic climax, whereas the succession of forests after human activity (e.g., fire, grazing, and soil deterioration due to over-cultivation) can result in adaptation of biotic climaxes [9]. Therefore, forest restoration that aids the recovery of forest structure, ecological functioning, and biodiversity towards those typical of a climax forest by the re-instatement of ecological processes is needed [31]. From an organism-centered perspective, developing forest management and exploitation regimes that mimic the natural conditions as closely as possible requires the determination of the degree to which typical species behaviors are responsible for the emergence of climatic climax [32][33][34][35][36][37].

2. Successional Categorization of Forest Tree Species in Lithuania

Lithuania (62,000 km²) is situated in the hemi-boreal climatic zone (i.e., the transitional zone from temperate to boreal forests) and is affected by the humid marine climate of the Baltic Sea [38]. The natural potential forest cover of Lithuania is predominantly composed of five main forest types: (i) hemi-boreal spruce forest with mixed broadleaved trees (55%), (ii) mixed oak–hornbeam forests (22%), (iii) boreal and hemi-boreal pine forests with partial broadleaved trees (18%), (iv) lime-pedunculate oak forests (4%), and (v) species-poor oak and mixed oak forests (1%) [39]. Thus, the natural climatic climax of the region for tree species consisted of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.) Karst), birch (*Betula pendula* Roth and *B. pubescens* Ehrh), alder

(*Alnus glutinosa* L. Gaertn. and *A. incana* L. Moench), English oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.), and European hornbeam (*Carpinus betulus* L.) [40]. Currently approximately 33% of Lithuania is forested with Scots pine, Norway spruce, and birch forming the dominating forest stand types [41]. The full range of hemi-boreal forest species found in Lithuania and their life history dynamics can be found in Table 1.

Table 1. A simplified framework for the life history dynamics for hemi-boreal tree species in Lithuania.

Tree species	Life history traits						
	Dominant Stand Proportion [41]	Soil Moisture A [42][43]	Soil Fertility B [42][43]	Shade Tolerance	Hardiness C [44]	Life Expectancy [43] (Harvesting age)[45]	Successional Strategy
	Dominant Forest Tree Species						
Scots pine (<i>Pinus sylvestris</i> L.)	34.6%	1–3 and 5	1–3 and 5	Intolerant	9	300–400 (110)	Disturbance generalist
Norway spruce (<i>Picea abies</i> L. Karst)	20.9%	3–4	3–4	Intermediate	7	200–300 (71)	Succession generalist
Silver birch (<i>Betula pendula</i> Roth)	22.0%	2–5	2–4	Intolerant	9–10	150 (61)	Disturbance generalist
Black alder (<i>Alnus</i>	7.6%	4–5	3–4	Intermediate	7	180–200 (61)	Disturbance generalist

<i>glutinosa</i> L. Gaertn)							
Grey alder (<i>Alnus incana</i> L. Moench)	5.9%	2–5	3–4	Intermediate	9	50–70 (31)	Disturbance generalist
Eurasian aspen (<i>Populus tremula</i>)	4.6%	3–4	3–4	Intolerant	9	80–100 (41)	Disturbance generalist
English oak (<i>Quercus robur</i> L.)	2.2%	3–4	3–4	Intolerant	6–7	500–600 (121)	Disturbance specialist
European ash (<i>Fraxinus excelsior</i> L.)	0.9%	3–5	4–5	Intermediate	7–8	> 300 (101)	Succession specialist
Other Secondary Native Forest Species							
Small- leaved lime (<i>Tilia cordata</i> Mill.)	0.4%	3	3–4	Intermediate	7	500–600 (61)	Succession specialist
Downy birch (<i>Betula</i>	0.4%	3–5	2–5	Intolerant	9	100 ^D	Disturbance generalist

<i>pubescens</i> Ehrh)							
European hornbeam (<i>Carpinus betulus</i> L.)	0.2%	3	3–4	Tolerant	5	200–300 (61)	Disturbance generalist
Norway maple (<i>Acer platanoides</i> L.)	0.2%	3–4	3–5	Tolerant	8	150–300 (101)	Disturbance specialist
White willow (<i>Salix alba</i> L.)	<0.2%	4	4–5	Intolerant	8	>100 (31)	Disturbance generalist
Bird cherry (<i>Prunus padus</i> L.)	<0.2%	4–5	3–5	Intermediate	9	150 ^D	Disturbance specialist
Crack willow (<i>Salix fragilis</i> L.)	<0.2%	4	4–5	Intolerant	8	75 (31)	Disturbance generalist
Field elm (<i>Ulmus minor</i> Mill.)	<0.2%	2–4	4	Intermediate	5	300 (101)	Succession specialist
European white elm	<0.2%	3–4	3–4	Tolerant	6–7	250–300 (101)	Succession specialist

(Ulmus laevis Pall.)							
Wych elm (Ulmus. glabra Huds.)	<0.2%	3–4	4–5	Tolerant	6	300 (101)	Succession specialist
Wild apple (Malus sylvestris L. Mill.)	<0.2%	4–5	3–5	Intolerant	8	300 ^D	Disturbance specialist
Wild pear (Pyrus pyraester L. Burgsd.)	<0.2%	3–4	3–4	Intermediate	6	200–300 ^D	Disturbance specialist
Introduced Species							
European beech (Fagus sylvatica L.)	<0.2%	3 ^[38]	3–4	Tolerant	5	500 (101)	Succession generalist
Sessile oak (Quercus petraea Matt. Liebl.)	<0.2%	3	2–3	Intermediate	6–7	500–600 ^D	Disturbance specialist
Large-leaved lime (Tilia	<0.2%	3–4	4–5	Intermediate	7	500–600 ^D	Succession specialist

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3. Conclusion

Each hemiboreal forest tree species can be represented by one of the four types of ecologically invariant life-history trajectories of species. Furthermore, disturbance generalists, specialists, successional generalists,

progressing towards the restoration of the climatic climax. However, further research is needed to develop the

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