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Succession and Dynamics of Norway Spruce Communities on Gulf of Bothnia Rising Coastlines

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Abstract

This thesis encompasses two approaches to primary succession on ground-moraine seashores undergoing land uplift, the directional succession from early stages via transitional broadleaf assemblages to late Norway spruce (*Picea abies* (L.) Karst.) forests, and the structure and dynamics of the old-growth, undisturbed spruce forest. A basic assumption made was that the constant and known (over the viewed time period) uplift rate provides a predictable ground age (temporal) sequence, which can be estimated by determining ground surface elevation above mean sea level. The studies were conducted within the Ostnäs (ca. 63°49'N, 20°41'E) and Sladan (ca. 63°51'N, 20°43'E) Nature Reserves in the Norra Kvarken Archipelago, coastal Västerbotten, northern Sweden. All study sites represented undisturbed successional sequences.

Main results and conclusions were the following: (*i*) Grey alder (*Alnus incana* (L.) Moench.), rowan (*Sorbus aucuparia* L.), juniper (*Juniperus communis* L.), and Norway spruce form six successional stages based on occurrence and composition, and three stages based on dominance, from early-successional alder to late-successional spruce. (*ii*) Spruce is able to establish after 30 to 40 years of succession, i.e. 25 to 35 cm above mean sea level. (*iii*) Depth of organic layer and cover of bottom layer vegetation and litter increase, while cover of field layer vegetation decreases, with time of succession. (*iv*) Diversity of field- and bottom-layer types, and spruce size categories, increase to a mode during mid-successional stages. (*v*) Patterns of dead spruce reveal two mortality occasions – self-thinning associated with early-successional competition, and stochastic mortality associated with late-successional, old-growth development. (*vi*) Spruce age pattern follows a positive, linear relationship with ground age, where spruce age pattern approaches one year per three years of ground age. (*vii*) Old-growth conditions can develop within 300 years from original site emergence above mean sea level.

The results are discussed with reference to basic concepts such as primary, secondary, allogenic, and autogenic succession, facilitation, directionality, colonization, and diversity. Consequences of the continuous landscape transformation owing to the land-uplift process are linked to the theory of island biogeography, and to the chronosequence approach to succession. It is argued that changing allogenic and autogenic factors maintain a continuous modification of the successional pathway, by affecting the lowest level of spruce establishment, hypothetically producing a curvilinear relationship between spruce age and ground age. Finally, some applications to forest management are elucidated.

Key words: Ground age, Land uplift, *Picea abies*, Primary succession, Structure, Tree age, Tree-species belt.

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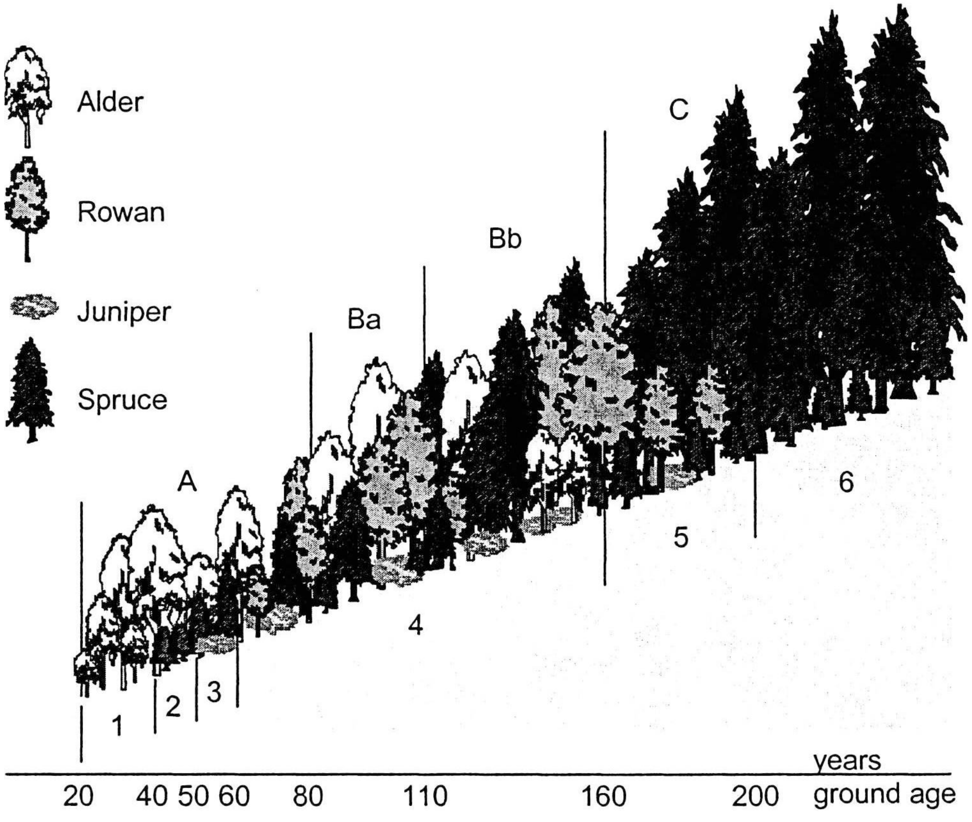

Fig. 1. *Successional stages of tree species belts on rising ground-moraine seashores, the Gulf of Bothnia. Stages 1 to 6 are based on species occurrence, and stages A to C on dominance (from Paper **II**).*

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Appendix

Papers I-V

This doctoral thesis is based on the following five papers, which will be referred to in the text by the corresponding Roman numerals.

I. Svensson, J.S. and J.K. Jeglum. 2000. Primary succession and dynamics of Norway spruce coastal forests on land-uplift ground moraine. *Studia Forestalia Suecica 209*. 32 pp.

II. Svensson, J.S. and J.K. Jeglum. Spatio-temporal properties of tree-species belts during primary succession on rising Gulf of Bothnia coastlines. (Manuscript.)

III. Svensson, J.S. and J.K. Jeglum. Primary succession pathway of Norway spruce communities on land-uplift seashores. (Accepted for publication in *Ecoscience*.)

IV. Svensson, J.S. and J.K. Jeglum. A chronosequence approach to the relationship between age of Norway spruce and ground age during land-uplift primary succession. (Manuscript.)

V. Svensson, J.S. and J.K. Jeglum. 2001. Structure and dynamics of an undisturbed old-growth Norway spruce forest on the rising Bothnian coasline. *Forest Ecology and Management 151*, 67-79.

Papers **I**, **III**, and **V** are printed with permission from the publishers.

Introduction

Conceptual and theoretical framework

Succession, which in its widest sense refers to "*observed sequences of vegetation associations or animal groups*" (Drury and Nisbet, 1973, p. 331), is one of the most fundamental concepts in ecology. Despite its early scientific recognition (by Buffon in 1685, according to Kimmins, 1997a; by Lancisi in 1714 according to Pignatti and Ubrizsy Savoia, 1989), and more than 150 years of rigorous scientific attention (review of work during the 19th century by Clements, 1916, and later work e.g. by Miles, 1987), succession remains a most confounding concept (McIntosh, 1981). Huston and Smith (1987, p. 168) devote the first sentence in their influential article to state that the "*continuing generation of hypothesis concerning plant succession suggest that this phenomenon is still not fully understood*". According to Pickett et al. (1987), this is owing to the lack of a general theory to which successional patterns and mechanisms can be related, to a poor focus of basic concepts, and to the limited scope and poor treatment by existing models. Debate, development of new ideas, and theories, as well as modifications and clarifications of older ones, is still continuing with unabated energy (e.g. Rydin and Borgegård, 1991; Chapin et al., 1994; Mann et al., 1995; Clark et al., 1998; Lichter, 2000), long after "*the bitter controversies of the 1920's*" (Langford and Buell, 1969, p. 128) between a more deterministic view on the successional pathway, advocated mainly by Clements (1916; 1928), and a more stochastic view, advocated mainly by Gleason (1917; 1926).

Primary succession has been a key ecological issue for more than a century (Binkley et al., 1997). According to one of the more original definitions by Clements (1904, p. 107), primary succession arises on "*newly formed soils, or upon surfaces exposed for the first time, which have in consequence never borne vegetation before.*" Primary succession occurs on substrates like elevating coastlines, river floodplains, volcanic deposits, sand dunes, and glacial forelands (Glenn-Levin and van der Maarel, 1992). Secondary succession, conversely, occurs on substrates which have been influenced by vegetation. Although current distinctions between primary and secondary succession are vague and somewhat disparate (cf. Kimmins, 1997a), a reasonable statement is that primary successions arise from a point in time and space where legacies of the past can be neglected with respect to their influence on ongoing ecological processes, whereas secondary successions arise from a point where such assumptions can not be made. Pickett (1989, p. 126-127) gave some thoughtful comments about the distinction between the terms 'past' and 'history'; "*... the past is comprised of the actual prior conditions, while history is the record of those conditions. Thus, all systems have a past, but not all systems have a history.*", and continued; "*This cautions ecologists to be aware of possible prior conditions even when there is no obvious record of them.*" The analog to succession is, accordingly, that primary successions at their initial stages have no past, nor any history, again with respect to the influence on ongoing ecological processes.

Two main areas of glacio-isostatic, elevating coastlines can be found on the northern hemisphere; the Hudson and James Bay areas, Canada, and the Gulf of Bothnia and White Sea areas, Fennoscandia (including parts of Sweden, Finland, Norway, northwest Russia and the Baltic states; see maps e.g. in Ekman, 1993). Despite similarities in glacial history and uplift rates, these two areas are very different in climatic, edaphic and topographic properties, and these differences greatly influence the biophysical ecosystem and landscape evolution. A comparative analysis of the two areas is under preparation by the author, and to summarize, the conditions in the Gulf of Bothnia area allow for much more rapid and vital ecosystem responses to the increase in land area. A climax-like, old-growth Norway spruce (*Picea abies* (L.) Karst.) forest can develop within two to three centuries of succession (Suomi et al., 1997; Svensson, 1998).

The Norra Kvarken Archipelago, Gulf of Bothnia (ca. 62°40' to 64°10'N and 19°10' to 22°20'E) (Fig. 1 in Paper **I**), provides an exceptional opportunity to study ecosystem development during primary succession. The highest present land-uplift rate, just north of the Norra Kvarken strait, amounts to 9.2 mm per year. Because of the low relief of coastal Västerbotten (Sweden) and Österbotten (Finland), large areas of land are added each year. Recent calculations by Michael Jones (unpubl.) tell that the islands of Björkö (2,340 ha) and Replot (3,879 ha) in Korsholms Archipelago, Finland, increased by 13.4 ha and 21.3 ha in land area per year, respectively. The figures were calculated for the period 1760 to 1890 (Björkö) and 1760 to 1942 (Replot). For further information about geological, ecological and other theoretical groundwork, I refer to Paper **I**.

A most attractive feature of these land-uplift successions is that dating of the temporal sequence, which in other examples of succession is problematic, *sensu* Jenny (1958) and Pickett (1989), is easily done and fairly accurate. Ground age can be calculated at any point along the shore-slope gradient, from elevation above mean sea level and the known rate of uplift; the higher the elevation the older the ground age. Another important feature is that seashore ecosystems and their successional, vegetation gradients are heavily influenced by a magnitude of factors which relate to intrinsic site properties, to properties in the environment (including sea water characteristics, sea level fluctuations and sea water movements), and to site location and position in the archipelago. This is essential to recognize, especially in view of the perpetual landscape transformation, which is caused by the ongoing land-uplift process, and which affects the relative degree of influence by these factors. One of the more critical factors is the sea-level fluctuations. The normal amplitude driven by atmospheric pressure and wind is 1.2 to 1.3 m in Norra Kvarken, with extremes as great as 2.5 m or more (Ericson and Wallentinus, 1979). (Ratan Hydrological Station, Norra Kvarken, reported 1.43 m over mean water level on February 23, 2002. Data provided by SMHI.) These aspects are further elucidated in the thesis chapter and in Papers **I** to **IV**.

Implications of knowledge about succession, structure and dynamics to forest management have been touched on in the thesis chapter and in Papers **I** and **V**. I use the terms 'nature-oriented forest management' or 'ecosystem management'. These terms belong to a family of terms which all denote a view in which the emphasis is placed on natural patterns and processes as basic management guidelines (see conceptual reviews, e.g., by O'Hara, 1998 and Hunter, 1999).

Statement of objectives

- To provide a general overview of the ecological significance of primary succession on rising ground-moraine seashores in the Norra Kvarken Archipelago (Paper **I**).

- To elucidate the successional pathway from early- to late-successional stages based on spatio-temporal properties of tree species on intermediate to less exposed seashores (Paper **II**).

- To describe the pathway of Norway spruce community development, from initial establishment to mature forest, by characterizing colonization levels, structural development, and diversity changes along successional sequences (Paper **III**).

- To analyze the relationship between Norway spruce age and ground age during succession, and to elucidate factors that influence this relationship (Paper **IV**).

- To assess structural and dynamic features of undisturbed, old-growth Norway spruce forests at late-successional stages, with respect to using such forests as references for nature-oriented forest management (Paper **V**).

Reconnaissance, study area, and study sites

The project started along two main lines, a literature review and a field reconnaissance. The literature review is included in this thesis as Paper **I**. The reconnaissance aimed to survey the coastal zone and to identify possible study locations. The study area was, for many practical reasons, the Västerbotten coastal area of Norra Kvarken. This area is undergoing land uplift at a rate of 8.4 mm per year (Topographic map Umeå 20K NO, Lantmäteriet, 1989). The focus was on upland, ground-moraine sites. There, the successional sequence terminates in a Norway spruce-dominated forest (Appelroth, 1948), which in the absence of disturbance forms a climax community (Papers **I** and **V**).

The reconnaissance resulted in the identification of 38 possible study locations, between the eastern shore of the Bay of Täftefjärden (ca. 63°45'N, 20°30'E) and the Bay of Mittifjärden (ca. 63°50'N, 20°45'E). I used eight different parameters to describe the locations: (*i*) estimated time of undisturbed succession; (*ii*) dominating tree species and belts (zones); (*iii*) initial establishment pattern of spruce seedlings (scattered or clusters); (*iv*) cohorts of smaller-sized spruce (infilling regeneration); (*v*) presence of wolf trees (large trees with open-grown crown structure); (*vi*) presence of deadwood; (*vii*) gap development at older stages; and (*viii*) gap regeneration. Parameters (*iv*) to (*viii*) solely concern the spruce-dominated stage. In addition, factors such as compass aspect of the shoreline, fetch, site isolation, available area (size), characteristics of the surrounding landscape, and land holder, were noted.

I selected four locations for the field studies, one within the Ostnäs Nature Reserve, and three within the Sladan Nature Reserve. The Ostnäs location consisted of three islands in a sheltered location on the shore of the semi-enclosed Bay of Sörjärden (ca. 63°49'N, 20°41'E). The islands are connected with each other and with the headland via coastal marshes and meadows. Each island became a study site: Ostnäs 1, 2, and 3 (Fig. 1). The Sladan locations (ca. 63°51'N, 20°43'E) were rearranged to represent a sequence of five study sites from high to low coastal exposure: Sladan 1, 2, 3, 4, and 5 (Fig. 1). The south tip of Österstgrundet peninsula faces the open sea of Norra Kvarken, and was selected to represent the highest exposure (Sladan 1). The south tip of Lillgrundudden Peninsula faces the broad opening of the large Bay of Ostnäs, a slightly less exposed site (Sladan 2), and its southwest (Sladan 3) and west (Sladan 4) shores represented two sites with decreasing exposure. The south shore inside the small and almost enclosed Bay of Sönnerstgrundsfjärden, represented the least exposed site (Sladan 5). All data presented in this thesis was collected in these eight study sites. For further presentation of the study sites, I refer to Papers **II** to **V**.

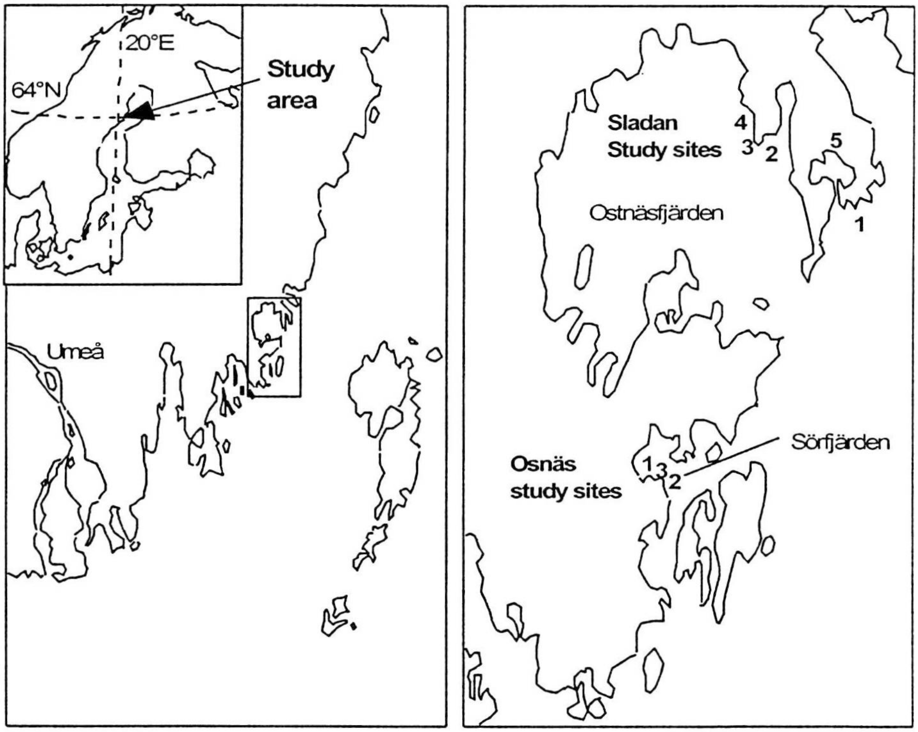

Fig. 2. *Location of research areas and study sites.*

A common practice of Swedish and Finnish coastal villages in the past was to establish a strip of community-owned land seawards from the private-owned land (Ristaniemi et al., 1997). The original reasons for this were to ensure public access to sea landings, and to allocate all new land among the land holders in a just way. In the village of Ivarsboda, on the Swedish side of Norra Kvarken, a border was set in 1856 (Rönnberg, 1998) which enclosed a continuous community-owned strip along the coastline. The vertical gain of land by the uplift has been some 1.2 m since then. The community-owned strip has in some instances been left for natural development. Undisturbed succession sequences to semi-mature, spruce-dominated stages are common in Ivarsboda and in other coastal villages, and sequences to climax-like, old-growth stages, although rare, can be found (Paper **I**; Svensson, 1998). The eight study sites are located on community-owned land, and all represent undisturbed sequences of primary succession, as far as can be detected.

Thesis

Many times a thesis chapter starts with a review of the theoretical and historical groundwork which is linked to the problems and questions addressed in the project. Here, a literature review is included as Paper **I**. This paper is treated differently from Papers **II** to **V**, because it forms their background. The review ends with a concluding section on 'identified research needs', which was developed into approaches and objectives. Materials and methods for Papers **II** to **V** are briefly outlined in a combined section below. I refer to the attached papers for further information about these matters. Also the main results and conclusions are presented in a combined section, and later discussed in the section 'Issues of current interest'.

Paper I – The literature review

The literature review is a general overview of vegetational and floristic changes during primary succession on the rising Gulf of Bothnia coastlines, with emphasis on Norway spruce succession, structure, and dynamics. Succession is not treated more broadly as the temporal change in any measure of ecosystem function, like energy, biomass, and nutrient cycling (cf. West et al., 1981). We elucidated natural forests and their potential as references for nature-oriented forest management, described the geological phenomenon of land uplift and the temporal sequences it provides, and presented our research area. We provided a general scheme on successional stages on ground-moraine seashores, and gave suggestions for terminology (Fig. 2). We also gave a review of central concepts and definitions, and a comprehensive overview of the literature on primary succession in the Gulf of Bothnia area and elsewhere.

A key conclusion was that apart from a few papers mainly by Ericson (1981a; b) not much has been published in the scientific forum. Primary succession sequences terminating in late-successional forests on boreal ground-moraine shorelines, and the influence of land uplift and other factors, have not been elucidated at all. Some research has been done further south, in coastal Uppland, central Sweden, and much of that compiled in the thesis by Cramer (1986). He dealt, however, mainly with other conditions and species.

We stated that attention should to be paid to the initial spruce seedling colonization relative to factors like water level, degree of exposure (winds, fetch), parent material, seedbed types, potential seed source (isolation), and island size. Pathways of Norway spruce primary succession relative to changes in autogenic site conditions and allogenic factors caused by landscape transformation deserve research effort. Attention should also be paid to how the spruce populations respond to site maturation, i.e. to increasing ground age, and to autogenic processes in spruce-dominated stages developing towards climax-like, old-growth forests.

It was concluded that the ongoing land uplift provides excellent successional sequences, and an exceptional opportunity to add new and important knowledge on original forest ecosystem development: (*i*) long-term, undisturbed forest seres terminating in a climax-like Norway spruce forests can be found; (*ii*) the mesic ground-moraine sites are generally quite productive; a well-stocked, old-growth spruce forest can develop within short ecological time; (*iii*) the undisturbed successional shore-slope sequence, going back to original soil formation at early stages, provides the possibility to estimate the history of community development; (*iv*) the relationship between surface elevation and land-uplift rate facilitates dating by estimates of ground age, and consequently allows a four-dimensional study approach; and (*v*) in view of the extensive anthropogenic influence in boreal Fennoscandian forests, the few remaining natural spruce forests should be recognized and carefully documented.

Based on the reconnaissance and the literature review, it became clear that from an ecological point of view, with the focus on the biotic component of forest ecosystems and on forest management aspects, two main approaches could be recognized – the directional succession from early-successional stages at the seashore via transitional broadleaf assemblages to late-successional spruce stages, and the intricate structure and dynamics within the late-successional, old-growth and undisturbed spruce forests. This PhD-project encompassed both approaches.

Outline of Papers II to V

The central question in **Paper II** was how tree species performance and belt characteristics depend on shore slope, and on spatial (distance) and temporal (ground age) properties (Table 1 and Fig. 2). The data was collected from ten transects (together encompassing 4,220 m^2) at five different study sites within the Sladan Nature Reserve. In total 4,108 individuals of tree species ≥0.5 m were sampled, across a temporal sequence ranging from about 20 to about 260 years of succession.

Norway spruce and its community is treated more specifically in **Paper III**. The successional pathways of spruce categories, i.e. size classes of live spruce from current seedlings to mature and dead spruce, and of surface organic layer, bottom layer and field layer types, were elucidated. Attention was devoted to the relationship among these community parameters and to diversity changes. Our results were discussed with reference to two influential hypotheses on diversity changes during succession; Margalef (1963) hypothesized that diversity increases to a peak during mid-successional stages but later declines to an intermediate steady diversity level during late stages, whereas Odum (1969) hypothesized that diversity increases to a steady high level in late stages. Data was collected in the same transects as in Paper II.

The temporal sequence provided by land uplift is highlighted in **Paper IV**, which utilizes the chronosequence approach to succession and is based on the relationship between age of Norway spruce and ground age. The ground-age dating procedure (described in the Introduction) allows for careful examination of how temporal changes influence the vegetation. The existence of a pure chronosequence, as it was defined by Jenny (1958), suggests that if spruce is able to establish on ground age of 30 years (Paper III), one would find a 100 year old spruce on ground-age 130-years. The results were based on a sample of 387 ground-age-positioned spruce trees, aged at ground level, at 0.25 m, and at 1.3 m above ground. The sample came from eight study sites within the Ostnäs and Sladan Nature Reserves.

The final paper, **Paper V**, elucidates the structure and dynamics of an undisturbed, old-growth and climax-like Norway spruce forest. The study was based on a 1,050-m^2 plot on an island in the Ostnäs Nature Reserve, which emerged from the sea fully

300 years ago. The emphasis was on the horizontal and vertical distribution of trees and shrubs. Interpretations of dynamics were based on a classification of health stages, which facilitated estimates of mortality rates, and hence allowed analysis of structural changes over time. We elaborated on spatial and temporal patterns in the view of this forest as a reference for nature-oriented forest management.

Main results and conclusions

We found that spruce seedlings were able to colonize after only 30 to 40 years of succession (25 to 35 cm above mean sea level), and that spruce height and size increased with increasing ground age (Fig. 6, Paper **II**; Table 2 and Fig. 3, Paper **III**). The figures presented on spruce colonization levels belong to the lowest ever reported for coastline conditions. It is evident that Norway spruce has the capability to cope with submergence, fluctuating water levels, ice scraping, and other seashore factors.

Four woody species – grey alder (*Alnus incana* (L.) Moench.), rowan (*Sorbus aucuparia* L.), juniper (*Juniperus communis* L.) and Norway spruce – occurred commonly and formed distinct belts (Table 3 and Fig. 3, Paper **II**). Alder and spruce were initially found below, and juniper and rowan in the vicinity of, the highest water level within the normal fluctuation amplitude.

Based on individuals ≥0.5 m tall, alder was initially found after 20 years of succession, spruce after 40 years, juniper after 50 years, and rowan after 60 years (Fig. 6, Paper **II**). Because of the longer time required by spruce to become a dominant species, the belt order was different from the order of initial occurrence, from alder to rowan to juniper to spruce. Juniper occurrence was less significant compared to the other species. The belt width decreased from alder to rowan to spruce, and with increasing shore slope (Fig. 4, Paper **II**).

We identified six successional stages based on tree-species (≥0.5 m) occurrence: (1) *alder*, 20 to 40 years; (2) *alder and spruce*, 40 to 50 years; (3) *alder, spruce and juniper*, 50 to 60 years; (4) *alder, spruce, juniper and rowan*, 60 to 160 years; (5) *spruce, juniper and rowan*, 160 to 200 years; and (6) *spruce* alone, from 200 years and onwards (Fig. 7, Paper **II**). Juniper was treated as the other species although it is almost always a shrub species rather than a tree species. We also identified three successional stages based on tree-species dominance, where one single species had more than half of the total number of individuals: (A) *alder stage*, 20 to 80 years; (B) *mixed stage* with decreasing alder, increasing and then decreasing rowan and juniper, and increasing spruce, 80 to 160 years; and (C) *spruce stage*, 160 years and onwards. These figures are relevant for ground-moraine shores on intermediate-exposed conditions in intermediate or inner parts of the archipelago.

The depth of surface organic layer gradually increased with elevation above and distance from shoreline, i.e. with time of succession (Table 1 and Fig. 5, Paper **III**). Because of the increasing cover of conifer litter on the ground surface in older stages (Fig. 1, Paper **III**), it is reasonable to assume that this is an autogenic effect of the *in situ* spruce population. In general, the field layer declined in cover with time of succession, while the bottom layer (mosses and litter) increased in cover (Fig. 1, Paper **III**).

The successional pathways of field- and bottom-layer types, as well as of spruce categories, followed unimodal trends of increasing and then decreasing diversity, rather than peaking in the oldest stages (Figs. 2 and 4, Paper **III**). Hypothetically, the peak in diversity at stages forming after 100 to 200 years of succession with respect to field- and bottom-layer types, and after 200 to 230 years of succession with respect to spruce categories, represent diversity modes that apply also to undisturbed temporal sequences that are longer-term than those sampled in this study.

We found two separate density peaks of dead spruce, indicating two separate mortality occasions; one after 130 to 140 years of succession, and one beyond 220 years (Figs. 3 and 5, Paper **III**). These two occasions relate to two different processes; self-thinning associated with early-successional competition, and stochastic mortality associated with late-successional old-growth development.

The Norway spruce age and ground-age relationship responded significantly to a positive, linear model in which spruce-age pattern approached one year per three years of ground age, viewed over three centuries of succession (Table 2 and Fig. 2, Paper **IV**). These results are reasonable and consistent with other related studies, but were based on a rather limited set of data, and should be regarded as a hypothesis for further investigation.

We discussed the chronosequence approach to succession (Paper **IV**), and found that a reasonable assumption is that all state factors – topography, climate, parent material, biota, and time (cf. Jenny, 1941; 1958) – may vary along any specific shore-slope gradient. This is a consequence of the ongoing landscape transformation by the land-uplift process, which leads to a continuous change in autogenic (e.g. seed source, seedbed conditions) and allogenic (e.g. exposure, isolation) conditions. This variation may then be reflected by the *in situ* vegetation on different successional stages along the shore-slope gradient. Continual changes in state-factor conditions cause a continuous modification in the successional pathway. With respect to Norway spruce seedling colonization, this affects the lowest level of spruce establishment on the seashores. Hypothetically, this leads to a positive, curvilinear relationship between spruce age and ground age (Fig. 3, Paper **IV**) along the shore-slope gradient. As conditions become more optimal for spruce seedling establishment on the most recently exposed ground, the curve approaches a 1:1 linear relationship, i.e. spruce migration rates are consistent with the land-uplift rate.

With respect to natural development of old-growth Norway spruce forests, we showed that old-growth conditions have developed within 300 years from original site emergence (Paper **V**). The forest displayed a dense, patchy, uneven-sized, and uneven-aged structure with high stocking levels of living trees and deadwood (Figs. 2 and 4, and Table 1 and 3, Paper **V**). Height and diameter followed a reverse-J size distribution, and age a normal distribution. The ongoing dynamic trend is the maintenance and/or amplification of a disorderly structure (Fig. 5). We concluded that a vertical stratification approach to structural description can provide relevant ecological insight for practical management applications.

Three main developmental phases were discerned (Paper **V**): (*i*) *Forest establishment phase:* Currently dominant trees established infrequently, scattered, and with low density during the initial 40+ years. (*ii*) *Multi-sized development phase*: A gap-filling (autogenic) influx occurred beneath and between the dominants during approximately 40 years, resulting in a closed, stratified forest. (*iii*) *Competition phase*: The influx of regeneration during the latest 30 years has been substantially reduced. The main trend has been a decrease in density owing to high mortality rates. It was hypothesized that the next phase of development would be a (*iv*) *Balanced phase*: An ecologically stable situation where mortality is balanced by recruitment.

Issues of current interest

The literature review was written at an early stage, and now, some years later, it still forms a good theoretical foundation, even though it has shortcomings. In this section I bring up some complementary literature and elucidate ideas that have evolved during the progress of my research. I refer to and discuss results from Papers **I** to **V**, in the context of future scientific prospects.

Primary or secondary succession, allogenic or autogenic succession

Glenn-Lewin and van der Maarel (1992, p. 14) stated that the distinction between primary and secondary succession is ambiguous; "*Primary succession seems easy to recognize, leaving all else to secondary succession*", and continued; "*Primary and secondary succession probably form a continuum*". The Gulf of Bothnia rising coastlines provide successions that can be defined as primary, or secondary, depending on which definition one would like to apply. Kimmins (1997a, p. 400), for instance, stated that primary succession "*begins in environments that lack organic matter and which have not yet been altered in any way by living organisms*." According to this definition, elevating seashores provide secondary successions because the sea is a living medium. Deposits of organic flotsam drift occur more or less everywhere along the shorelines, and may to some degree influence the shoreline parent material and, hence, the establishment and germination conditions for terrestrial species. In Paper **IV**, we showed that organic matter was present at early stages of succession, and discussed whether the matter was an allogenic deposition or an autogenic formation.

It is reasonable to assume that a gradient from a more to a less exposed site also represents a gradient from a more primary to a more secondary type of succession (Paper **I**), because of less accumulation of allogenic matter, and more re-allocation and erosion, with increasing exposure. For the same reasons, the more steep the shore slope, the more likely does a primary type of succession arise. Low-lying and gentle sloping coastlines, then, support a more secondary type, sometimes developing towards a peat-dominated community (Åström, 2001). The effect of slope on the tree-species belt performance was elucidated in Paper **II**, where we concluded that slope influences the performance and characteristics of tree-species belts.

Another characteristic of primary successions is that colonizing organisms arrive by migration (Fenner, 1987; Sauer, 1988). Migration patterns, low nutrient availability in early stages, and slow progress of succession produce a pathway that displays a more pronounced sequence from early to later plants (Drury and Nisbet, 1973; Gorham et al., 1979), i.e. a more obvious relay floristic mechanism (Egler, 1954). Plants migrate downward on the rising coastlines both by vegetative and generative propagules (Paper **I**). Ericson and Wallentinus (1979) pointed out that the steeper the topography, the more favored are species with vegetative capacity. Hence, on steep slopes species tend to spread vegetatively rather than by seed migration, i.e. an initial floristic feature

(Egler, 1954). According to this reasoning, and in contradiction to the statement made in the previous paragraph, secondary types of successions are likely to arise on steep sloping shorelines, and more primary types on gentle sloping.

Drury and Nisbet (1973) stated that primary successions are rare in nature and that very few cases have been observed, and if they have only early stages have been described. Ideas about later stages of primary succession are conflicting and hypothetical (ibid.). The primary succession on rising ground-moraine coastlines in the Gulf of Bothnia area is directional, from an early, open coastal meadow stage to a late spruce-dominated forest stage (Papers **I** to **IV**). Inside the spruce-dominated stage, however, it is not (Paper **V**). There, because of the inherent tendency of spruce forests to develop towards uneven-sized and uneven-aged communities (e.g. Kuuluvainen et al., 1998; Lähde et al., 1999; Kellomäki, 2000), the spatial variation and temporal change is owing to a patch dynamic regime (Pickett and White, 1985), which is stochastic and non-directional.

With respect to the nature of the rising-coastline successions, several arguments can be made. It can be argued that the primary succession ends at some stage of spruce forest development, because of the evident change in the directionality of the successional pathway. It can also be argued that the primary succession continues, because no major disturbance occurs to revert the succession back to an earlier stage, and hence to initiate a secondary succession. The primary succession, then, terminates in an infinitely prolonged phasic equilibrium (Watt, 1947), or climax; "*in which the composition of the biota remains approximately constant for a long period of time*" (Kimmins, 1997a, p. 401). It can also be argued that it is the main successional mechanism that changes, rather than the directionality of the successional pathway.

Tansley (1935) distinguished between autogenic succession, where the mechanism is internal and caused by interactions between biotic and abiotic ecosystem components and their environment, and allogenic succession, where external mechanisms act. Miles (1987) and others have noted that both types are likely to play a role in most cases of succession, and that their relative importance usually varies. The land-uplift process changes site conditions and causes corresponding changes in species composition. Hypothetically, each site changes until a stable moisture regime is reached, where the soil moisture that is retained is in balance with climate, parent material, position on slope, and biota (cf. Jenny, 1941). At this point the autogenic mechanisms and *in situ* vegetation and soil control of the temporal change are dominant over allogenic mechanisms (cf. Viereck et al., 1993; Klinger and Short, 1996). It can be argued that the switch from a directional to a non-directional pathway somewhere and sometime inside the spruce stage, represents the transition between allogenic succession and autogenic succession.

Using the concepts of primary, secondary, allogenic, autogenic, etc., is a helpful way to organize ones thinking and interpretation of succession. Elevating seashores have been listed many times as examples of situations that provide primary successions (e.g. Clements, 1904; Glenn-Lewin and van der Maarel, 1992). It is also common to find that this term has been used for specific studies in the Gulf of Bothnia area (e.g. Vervijst and Cramer, 1986; Carlsson et al., 1990; Tapper, 1993; Ecke and Rydin, 2000).

Facilitation, landscape transformation, and the temporal sequence

A fundamental principle in the deterministic view on primary succession was that facilitation had major importance (e.g. Clements, 1916; Odum, 1969; Tilman, 1985). Facilitation "*is the process by which colonizing species improve the environment for later successional species and, in the process, place themselves at a competitive disadvantage.*" (Chapin et al., 1994, p. 150). The basic idea is that accumulation of organic matter and its contained nutrients (sometimes with nitrogen enrichment by nitrogen fixers), facilitate establishment conditions for late-successional species (e.g. Mortimer, 1987; Bégin et al., 1993; Jumpponen et al., 1999). Proposed mechanisms for facilitation include micro-climatic as well as physical and chemical soil properties (Jumpponen et al., 1998).

The importance of facilitation as an overall mechanism has been questioned, however. Support is accumulating for a much more complex, stochastic view on succession (cf. Botkin, 1979), where factors such as competitive inhibition, tolerance, and life-history traits (seed production, migration patterns, growth rates, age at first reproduction, height development, and longevity) are of major importance (e.g. Drury and Nisbet, 1973; Connel and Slatyer, 1977; Huston and Smith, 1987; Miles, 1987; Fastie 1995; del Moral et al., 1995; Binkley et al., 1997; Lichter, 2000). The concept of facilitation applied on the rising seashores is closely linked to the ongoing landscape transformation, and to the temporal sequence of succession (Paper **IV**).

The seashore is a complex and hazardous habitat for terrestrial plants. The successional pathway that arises is a consequence of a magnitude of mechanisms (factors). To understand the rising-coastlines successional pathway towards Norway spruce-dominated forest, it is necessary to interpret the succession in terms of allogenic and autogenic mechanisms. Allogenic mechanisms operate during both long- and short-terms. The long-tem allogenic mechanism is the steady, slow land uplift, which affects factors such as: topography and ground age; the proportion between land-area and sea area; potential biotic seed sources; landscape fragmentation and connectivity; fetch; isolation; mesoclimate (mainly wind); and groundwater level. Short-term allogenic mechanisms relate to the fluctuating water level (changing moisture conditions, re-allocation of organic and inorganic matter, ice scraping), and to water movements (waves, shore currents, erosion). Autogenic mechanisms relate to factors that operate internally at a specific site. Here one may list the state factors given by Jenny (1941): climate, topography, parent material, biota, and time. The influence on soil and vegetation at a specific site by the autogenic factors depends, to a substantial degree, on the influence of the allogenic factors.

It is most important to emphasize that as land uplift goes on, the relative influence of the above-mentioned allogenic factors changes. Islands and peninsulas continue to rise around a specific site, changing the proportion of land area and sea area, and affecting site conditions. The exposure of a specific shore may change (decrease) over time because of changed (increased) relative shelter. Hence, the structure and composition of vegetation and soil on different levels (or ground ages) along a shore slope, reflect gradually changing conditions.

In Papers **II** and **III** we presented the successional pathway by giving tree-species belts and Norway spruce community development relative to elevation above mean sea level and time of succession. The study sites were on intermediately exposed headland shores in intermediate and inner parts of the archipelago. There, we can assume that effects of isolation are minimal with respect to potential seed source. In Paper **IV**, we discussed that at more sheltered and at more exposed sites, as well as at more isolated sites (islands), the successional pathway may differ from what we have found. Slaney (2001), in her Master's Thesis conducted at the Sladan sites, showed that the bottom-layer and field-layer composition, as well as spruce-seedling distribution and modal occurrence, are both affected by exposure; the less the exposure, the further seaward are comparable zones.

In Paper **I** (Fig. 4) we discussed the hypothesis proposed by Appelroth (1948), who stated that the natural primary succession will continue beyond the Norway spruce stage into a Scots pine (*Pinus sylvestris* L.) stage. A lowering groundwater table as uplift goes on would decrease site richness and favour natural establishment of the more drought tolerant pine. In the Norra Kvarken Archipelago, pine sometimes form stands on the top of islands or peninsulas where the soil cover is more shallow. My impression is that pine forests result either from disturbances (e.g. clearcutting in the past; fire; wind; over-grazing) or from a separate successional pathway. In Paper **I**, we suggested that such pine forests are original on the xeric tops of some islands, and not involved in the normal primary succession along the mesic shore slopes. In a long-term perspective, however, spruce will also enter these sites.

In Paper **IV**, we elaborated on the relationship between age of Norway spruce and ground age, by applying the chronosequence approach to succession. In a 'pure chronosequence', as it was defined by Jenny (1958), the factor time should be the only one to vary, while the other state factors (climate, biota, parent material, and topography) should be constant. Accordingly, a reasonable interpretation is that if spruce is able to establish on ground age of 30 years (Paper **III**), one would find a 100 year old spruce on ground age 130 years. We came to the conclusion that age of Norway spruce and ground age significantly responded to a linear model. But we also found that a one-year increase in ground age did not result in a one-year increase in spruce age, but rather in a 0.3- to 0.4-year increase.

In our attempts to explain this delay in spruce age compared to ground age, we discussed (Paper **IV**) that along any specific primary succession gradient, the relationship between age of Norway spruce and ground age may not be linear (cf. Svensson, 2000). The landscape transformation generally leads to increasing shelter and less impact of allogenic disturbances. This results in more favorable conditions for spruce establishment on lower levels on the seashore, and to increasing potential seed source (autogenic and allogenic) providing greater numbers of seeds. Because of this continuous site facilitation, with respect to spruce establishment and germination, spruce age hypothetically follows a curvilinear relationship with ground age (Fig. 3, Paper **IV**). The curve indicates that spruce age approaches a 1:1 linear relationship with ground age when all conditions and state factors are optimal with respect to spruce establishment. At this stage, the rate of successional downward spread by spruce is consistent with the land-uplift rate. A Master's Thesis is presently under preparation: 'Initial Norway spruce colonization and early forest development during primary succession on islands undergoing land uplift' (Ingrid Sandström, unpubl., Department of Silviculture, SLU). She recorded spruce performance on 23 different islands in the Norra Kvarken Archipelago. The results tentatively support this curved relationship; spruce colonization level (compared to mean sea water level) increase with decreased isolation and decreased distance to seed source, and with increased island area and age.

The 'facilitation – landscape transformation – temporal sequence *continuum*' needs to be acknowledged to understand the primary succession pathway on the rising coastlines, and to thoroughly interpret ongoing ecosystem processes.

Island biogeography, colonization, and biodiversity

Islands have attracted great interest among ecologists, from the earliest naturalists to the present day researchers. A bench-mark was the compilation of the island biogeography theory by MacArthur and Wilson (1967). This theory states that the number of species on an island relates to three factors: area (size), isolation, and age, in given order of importance (Forman and Godron, 1986). Factors like habitat heterogeneity, site productivity, and disturbance regime also should be regarded, however (MacArthur, 1965). Rydin and Borgegård (1988) concluded in a study from Lake Hjälmaren, central Sweden, that small islands reach equilibrium levels of diversity later than large islands, because of disturbance by wave action and slow processes of substrate formation. Forman and Godron (1986) noted that the role of area and isolation has been thoroughly confirmed. Löfgren (2001), for instance, found that area and isolation were the important factors explaining species number on islands in the Stockholm Archipelago, central Sweden. Forman and Godron (1986, p. 103) also stated that age is the least well-documented factor, but seems to be "*a logical hypothesis*".

The rich archipelago and shallow depth of the Norra Kvarken strait allow for dramatic landscape transformation within short ecological time. Viewing a single island, all three main factors identified in the island biogeography theory vary over time; the island becomes larger, less isolated, and older. The Gulf of Bothnia rising coastlines provide an excellent opportunity to increase knowledge about the processes acting on patterns of diversity among plants and animals during ecosystem development from initial stages. In addition, metapopulation development owing to isolation of plant populations (*Silene dioica*; Giles and Goudet, 1997) should be mentioned.

The majority of higher plant species colonize islands by seed dispersal (Fenner, 1987). Wind is probably the main agent for distribution in most cases, but water, birds and animals should also be considered. The effectiveness of seed dispersal depends on five different factors (van der Valk, 1992): (*i*) seed production; (*ii*) vector of seed transport; (*iii*) timing of seed release; (*iv*) distance of dispersal; and (*v*) fate of dispersed seeds. Sjörs (1971) stated that there generally is a logarithmic decrease in propagule density with distance between seed source and target site. In his study in the Stockholm Archipelago, Löfgren (2001) found that colonization rates of grassland plants were positively correlated with island area. He suggested that this was an effect of habitat diversity, target area for dispersed propagules, parent material (soil depth), and climate (light conditions). He found no correlation, however, between colonization rate and distance to mainland. The diversity along successional sequences on islands in the Norra Kvarken Archipelago is at present undertaken as a Master's Thesis: 'A biogeographic approach to species richness and diversity on islands undergoing land uplift and primary succession' (Johanna Ydringer, unpubl., Department of Forest Ecology, SLU). Tentative results indicate that species richness, increase with decreased isolation and decreased distance to seed source, and with increased island area and age.

Diversity in ecosystems undergoing succession has received substantial scientific attention over the years. According to Grime (1977), the sequence of species composition along a successional gradient can be explained by how species can cope with stress and disturbance. Because these factors vary with time of succession (i.e. distance from and elevation above mean sea level), a gradual compositional change appears, reflecting the gradual change in stress and disturbance. Seedlings close to the shoreline suffer from severe stress. In their study on seashore meadows in northern Gulf of Bothnia, Ecke and Rydin (2000) found that the earliest species on seashore meadows in northern Gulf of Bothnia are clonal dominants or stress-tolerators. The importance of 'safe sites' (microsites suitable for germination and establishment) and abiotic factors characterizing them have been stressed in primary succession, but have rarely been studied (Jumpponen et al., 1999) and need further attention.

It is well established that habitat diversity controls species diversity to a great degree (e.g. Smith, 1972). In Paper **III**, we documented field and bottom layers, and spruce category diversity along transects from early, open stages to late spruce-dominated stages on headland shores. We found that field- and bottom-layer diversity mode occurred early, after 100 to 200 years of succession, and that spruce category diversity mode occurred slightly later, after 200 to 230 years. These modes coincide, roughly, with stages where woody species diversity was highest (Paper **II**), i.e. in the transition from alder to spruce. Thus, the diversity changes tended to follow the Margalef (1963) hypothesis rather than the Odum (1969) hypothesis on diversity trends during succession (Paper **III**), *sensu* Drury and Nisbet (1973, page 355) who concluded that high diversity is not "*an exclusive property of the later stages of vegetation succession*". A diversity trend with its mode during the later part of the successional transition from broadleaf to spruce is a reasonable general pattern on ground-moraine rising shorelines, probably also over longer-term successional sequences than accounted for in our studies, given the absence of larger-scale disturbances.

I suggest that the emergence, growth, and aging of islands in the rising Norra Kvarken Archipelago provide excellent opportunities to develop knowledge on the 'island biogeography – colonization – diversity *continuum*', especially with reference to the development of forest communities.

Applications to forest management

Succession, according to Connell and Slatyer (1977) is the process of community recovery from a disturbance which opens up a large area. They noted two critical factors, the rate of recovery to a state similar to the original state, and the degree of similarity in species composition, and continued (p. 1132); "*In terms of the management of either natural or disturbed sites, the correct plan to encourage a quicker recovery from perturbation depends on the type of community it is desired to develop and upon the likely model pathway that succession would follow.*" In fact, they touched on one of the central concepts in what later became termed 'sustainable forestry', the rapid recovery by stand internal and advanced regeneration after cutting (Kimmins, 1997b; Kellomäki, 2000). Sustainability, defined by Farrell et al. (2000, p. 6) is "*the ability to maintain productivity indefinitely with no net decline, even if the forest is subject to stress and perturbations.*" Kimmins (1997a, p. 397) elaborated on the evident links between succession and forest management; "... *much of a forest manager's life is spent manipulating succession. It is therefore extremely important that foresters have a sound grasp of this topic.*"

One implication of the rising coastlines primary succession to forest management is the potential use of the alder-spruce transition (Papers **II** and **III**) as a reference for reforestation of excavated or heavily disturbed soils. This aspect is linked to the facilitation concept discussed above, but more strictly to the nitrogen amendments by biological fixation. In addition to grey alder, the rising coastlines also commonly host other woody nitrogen fixers, like sea buckthorn (*Hippophaë rhamnoides* L.) and sweet gale (*Myrica gale* L.). Fisher and Binkley (2000) touched on the idea of alternating rotations of nitrogen-fixing trees and crop trees, or mixing both in one rotation, but noted that stand prescriptions still are hypothetical. They referred to a study by Miller and Murray (1979) who recommended 50 to 100 red alder (*Alnus rubra*) per hectare in a Douglas fir (*Pseudotsuga menziesii*) stand. Alder nodules contain the actinomycete *Frankia*, which fixes relatively high amounts of nitrogen; over 40 kg per ha annually has been reported for grey alder (Fisher and Binkley, 2000).

Another and a more fundamental issue is the paradigm shift in forest management, which is ongoing since a decade or so and evident to all of us. The shift encompasses a range of alternative conceptual approaches to forest management, developed on a firm knowledge base of natural ecosystem processes (e.g. Kimmins, 1997b; Norokorpi et al., 1997; Barnes et al., 1998; O'Hara, 1998; Hunter, 1999). The concept encompasses, fundamentally, the maintaining of large- and small-scale structural heterogeneity on a spatial and temporal basis, using management practices that favor the maintenance or amendment of structural diversity and long-term ecosystem sustainability (Chapin et al., 1996; O'Hara and Valappil, 1999). A current consensus is that a possible route towards management under these constraints is to use an operational system that simulates the natural forest structure, and that is applied within the natural ecosystem dynamics regime (e.g. O'Hara, 1998; Hunter, 1999; Lähde et al., 1999; Mason et al., 1999).

Much of the debate concerns the biodiversity of forest ecosystems. High biodiversity levels are thought to indicate vital ecosystems, and a maintained biodiversity level under a management regime, accordingly, is thought to identify a desirable operational system (e.g. Simberloff, 1999; Andersson et al., 2000). Smith (1972), Kuuluvainen (1994), Dale (1999), and others have argued that forest community stability and species diversity primarily are products of spatial heterogeneity. There is, however, a need for firm background knowledge on the spatial structure of natural forests as basic input to the development of management strategies (Franklin, 1997; Norokorpi et al., 1997; Barnes et al., 1998; Hagner and Nyquist, 1998).

In Paper **V**, we elaborated on the spatial structure and dynamics of an undisturbed, old-growth Norway spruce forest and discussed stages of forest development. In agreement with previous statements, for instance by Moeur (1993), Kuuluvainen et al. (1998), and Dale (1999), we concluded that analysis of spatial patterns in natural forest communities is a valid and important requirement for better understanding of forest management potentials. Forest ecosystem research is central to the development of forest management strategies (Farrell et al., 2000; Kellomäki, 2000). Key problems are to define natural forest structure and diversity at different scales (stand – landscape), and to transform ecological ideas into practical and effective tools (Simberloff, 1999; Kellomäki, 2000).

Much work remains, however. In a recent publication, Farrell et al. (2000, p. 15) stated that "*the entire concept of sustainable forest management ... needs to be revisited and regularly reviewed. The principle is clear, but neither the scope nor the temporal aspects of its application have been adequately explored.*"

Final remarks

This thesis summarizes empirical and descriptive research on primary succession terminating in late-successional Norway spruce forests, and on structure and dynamics of undisturbed, old-growth spruce forests. The obvious lack of a scientific base has been challenging, but also to a great degree determined the direction of this project. Many times during this thesis work I have felt that I am where Cowles was in the 1890s (Cowles, 1899) on the Lake Michigan sand dunes, or where Cooper was in the 1920s (Cooper, 1923) in Glacier Bay, without the intention to imply that this work is anywhere as influential. Hence, the most urgent research task, as I saw it, was to create an empirical foundation for future experimental research. I believe that the main value of this thesis is that it does provide just that.

The primary succession pathway on rising ground-moraine shores in the Norra Kvarken Archipelago is basically directional and predictable, but a more careful examination reveals a complex and stochastic pathway which does not permit explicit generalizations. The work that I present here was based on a rather limited set of data from few areas, and should be viewed mainly as a reference for future work.

The rising coastlines provide excellent examples of ecosystem development from original stages to late-successional forests. Perhaps the most significant aspect lies in the inherent and continuous landscape transformation, which results in continuous changes in factors that relate to ecosystem processes.

I wish the Swedish and Finnish governments good luck in their nomination of Norra Kvarken to the UNESCO World Heritage List. I trust that a successful application will result in a scientific attention that the rising coastlines rightfully deserve.

"*We must purge our minds of all prejudices, of all preconceived ideas, of all theories – of all those superstitions, or 'idols', which religion, philosophy, education, or tradition may have imparted on us. When we have thus purged our minds of prejudices and impurities, we may approach nature. And nature will not mislead us.*"

Francis Bacon

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