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The forest regeneration puzzle

Biological mechanisms in humus-layer and forest-vegetation dynamics

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Introduction

The tendency for managed coniferous forests to fail to regenerate naturally is a worldwide problem,
especially in areas with severe climates, such as mountain and boreal zones (Sirén 1955, Mayer
1976). Because most of these ecosystems produce high levels of field- and cryptogamic-layer biomass
(Persson 1980, Grier et al. 1981), it has been suggested that failure of coniferous forests to regenerate
is somehow related to the ground vegetation and the related soil organic components. Although

1 neglected by theoreticians, we may also assume that ground and below-ground organisms are
2 involved in the processes by which disturbances and the resulting plant successions maintain these
3 ecosystems (Finegan 1984).

4
5 Forest ecosystem dynamics have long been explained by changes in floristic composition (Foster
6 1988) and nutrient availability (Vitousek 1984). The passage from pioneer to late-successional plant
7 communities has frequently been modelled (McCook 1994) and in a few instances studied
8 experimentally (Facelli and Facelli 1993). Generally interactions between plants (including their
9 immediate environment as a passive partner) have been considered responsible for forest succession.
10 However, the below-ground components of any given ecosystem must also be taken into account
11 before successional and steady-state patterns in plant communities can be fully understood (Cromack
12 1981, Miles 1985; Nilsson 1994). A new emphasis on the study of forest ecosystem dynamics is
13 emerging, in which new field and laboratory techniques are used to study biological processes related
14 to plants and their interactions with soil. Although most of these studies bear only upon particular
15 aspects of forest regeneration, we have tried to assemble these pieces into an integrated view of the
16 regeneration puzzle. We focus mainly on European forests, because some major traits of American
17 forests, for example the absence of native lumbricid earthworms (Fender and McKey-Fender 1990),
18 may have a far-reaching influence on their dynamics.

19 20 **The framework of forest dynamics**

21
22 Forest regeneration, the establishment of a new tree cohort, normally occurs during succession that
23 involves plants, animals and microbes (Watt 1947, Cromack 1981, Finegan 1984, Oldeman 1990,
24 Bernier and Ponge 1994). The first stages of the life of a tree (the seedling and the sapling stages) are
25 dominated by strong environmental influences: intra- and inter-specific competition, and environmental
26 stresses. Once the tree is firmly established, it increasingly influences its own environment, both
27 above-ground, by shading and by intercepting rain, and below-ground, by absorbing water and nutrient
28 ions, and releasing other ions and organic chemicals. Softwood as well as hardwood trees tend to
29 acidify the soil because proton production, due to uptake and storage of nutrients by trees, exceeds
30 proton consumption, due to mineral weathering, mineralization of organic matter, and nitrogen fixation
31 in the soil (Ulrich 1986, Binkley and Richter 1987). The development of moder humus, that is, the

1 accumulation of organic matter in the form of the faeces of invertebrates deposited at the surface of
2 the soil profile, occurs as forest trees go through the phase of intense growth, the pole stage (Bernier
3 and Ponge 1994, Ponge and Delhaye 1995). At this time in their growth, most tree species may be
4 classed as soil acidifiers, except those that are able to reverse acidification through symbiotic nitrogen
5 fixation (Tarrant and Miller 1963) or by producing litter that decomposes at a high rate (Tamm 1990).

6
7 In old-growth forests, mull humus, defined by the abundance of earthworm faeces in mineral horizons
8 and rapid incorporation of litter, has been detected under adult trees, even under acidifying species
9 such as Norway spruce or European beech (Page 1974, Bernier and Ponge 1994, Ponge and Delhaye
10 1995). This change in organic matter decomposition is a key component of regeneration patterns. Any
11 process by which the accumulated forest organic matter is decomposed before the trees die, thus
12 making nutrients available to seedlings, will facilitate forest renewal. The low light intensities that limit
13 understory growth will diminish as large trees fall and gaps open in the canopy, which will improve
14 photosynthesis and thus growth rates of seedlings and saplings. However, a delay in the establishment
15 of new tree cohorts, for instance during unfavourable weather, might allow more competitive plant
16 communities to develop, including heath, grass, fern, or moss carpets, which generally impede the
17 establishment (Figure 1) or even the growth of tree species (Messier and Kimmins 1990, Ohlson and
18 Zackrisson 1992, Bernier and Ponge 1993, Dolling 1996, Zackrisson et al. 1997).

19
20 Thus important mechanisms influencing forest renewal operate through the soil system, including leaf
21 litter, and through ground vegetation (Nilsson et al. 1996). Knowledge of these mechanisms can
22 improve the ability of models to predict forest dynamics and climate-ecosystem interference (Wissel
23 1991, Andersson et al. 1996).

24 25 **Soil microorganisms**

26
27 Trees of nearly all species have their roots sheathed with soil ectomycorrhizal fungi, which play an
28 important role in nutrient and water uptake. The need for ectomycorrhizal symbiosis for the trees to
29 establish and grow well has long been known (Handley 1963). More recently, it has become clear that
30 the predominant ectomycorrhizal fungal species tend to change throughout the successional
31 development of forest stands (Mason et al. 1983, Gibson and Deacon 1988).

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Changes in humus form during forest development may explain the accompanying succession of mycorrhizal fungi. For instance successions of mycorrhizal toadstools have been observed during the colonization of calluna heathland by birch trees, together with a shift from mor (slowly decaying litter with a poor comminution by fauna) to moder humus (Miles 1985). Temperate-zone late-successional forest trees such as spruce (*Picea abies*) and beech (*Fagus sylvatica*) often regenerate on mull humus (Ponge and Delhaye 1995, Bernier and Ponge 1994). By contrast, rapidly growing trees (the pole stage of these species) are commonly associated with moder humus. This association may explain why early stage fungi (which normally live in mull humus) are succeeded by other species during stand development. The fine root system of trees in moder humus is nearer the soil surface than is found in mull humus (Meyer and Göttsche 1971), which probably selects for ectomycorrhizal fungal strains that are able to live preferentially within litter layers (Rose et al. 1983). The physical disturbance of horizons resulting from the burrowing activity of earthworms and associated animals (moles, small rodents) observed under mature trees (Bernier and Ponge 1994, Ponge and Delhaye 1995) may help to explain the return of early successional mycorrhizal fungi.

Only few species and genotypes of fungi that can live symbiotically with trees as ectomycorrhizae are reported in ericaceous heathland with mor humus (Read 1991). This reduction in the ectomycorrhizal pool, despite sufficient dispersal of spores by wind or animals, will contribute to impede forest tree establishment when ericaceous species are present (Handley 1963, Zackrisson et al. 1997) and thus will preclude or considerably delay the renewal of forest ecosystems when gaps are invaded by these species (Dighton and Coleman 1992).

Biochemical interactions

The growth and well-being of plants, animals and microbes can be favoured or inhibited by biochemical interactions with secondary metabolites. Vascular plants generally produce cocktails of different organic compounds, some of which may be waste products though many may be produced deliberately to make the plants unpalatable or toxic to herbivores (Zucker 1983). These compounds can be excreted (e.g., oils, waxes, resins), incorporated into cell walls (e.g., lignin, bark tannins), or enclosed in vacuoles within living cells (e.g. soluble tannins). When the plant tissues and organs die,

1 these organic compounds are liberated in the course of decomposition. In the meantime other inputs of
2 secondary metabolites occur by leaching of living parts. Certain of these compounds can affect other
3 organisms directly, and all can undergo biochemical reactions which alter humus properties. Below-
4 ground processes involving secondary compounds seem to be important in multi-species interactions
5 (Christy 1986, Hester et al. 1991). Thus seed germination and seedling growth can both be inhibited or
6 stimulated by organic compounds produced by living vegetation (Nilsson and Zackrisson 1992, Gallet
7 1994) or by litter and humus layers (Alvarez et al. 1979, Mallik and Newton 1988). These effects have
8 been assessed in laboratory experiments in which root competition effects were controlled for (Nilsson
9 1994). This biochemical control primarily affects the development of the root system of young tree
10 seedlings, but also ectomycorrhizal fungi and other soil microorganisms (Robinson 1972, Baldwin et al.
11 1983, Nilsson et al. 1993). Phenolic compounds, which are particularly abundant in the Ericaceae and
12 their allies, have often been implicated in these interactions, and their effects can be indirect, through
13 the binding of protein or other nitrogenous compounds (Howard and Howard 1990).

14
15 Biochemical interactions among organisms can thus help to explain successional patterns nearly as
16 well as do changes in resource availability, which are well-established theoretically (Heard 1994) but
17 poorly documented experimentally. However, in terms of biochemical control between plants, it can be
18 difficult to extrapolate results from laboratory to field conditions, because the properties and
19 persistence of biochemical compounds are strongly influenced by the soil conditions. For instance,
20 humus condition and fires can modify biochemical interactions between plants. Also, some plant
21 secondary compounds detrimental to other plant species or soil organisms can be adsorbed on soil
22 particles with a high surface area such as clay (Mortland et al. 1986), which may explain why soil
23 biological activity and plant growth may be enhanced by the artificial (Salonius 1983) or natural (Haimi
24 et al. 1992) disturbance of soil horizons. Similarly the decreased biochemical interference after a
25 forest-fire may partly be explained by the production of charcoal which, like clay particles, acts as a
26 detoxifier and a catalyzer in soil (Zackrisson et al. 1996).

28 **Decaying wood and regeneration of coniferous species**

29
30 The importance of rotting wood as a rooting medium for the establishment of coniferous trees such as
31 spruce (*Picea* spp.) and hemlock (*Tsuga* spp.) has been widely documented for different ecosystems,

1 especially under harsh climatic conditions (McCullough 1948, Harmon and Franklin 1989, Hofgaard
2 1993, Hörnberg 1995). Rotting wood has the remarkable property to adsorb or fix small organic
3 molecules. This phenomenon stems from the aromatic nature of its main constituent, lignin, which
4 becomes less bonded to cellulose as decomposition proceeds (Highley and Kirk 1979) and thus
5 becomes open to chemical reactions. Despite structural changes with time, lignin remains polymerized
6 (Kirk and Chang 1975) and acts as a binding agent for water-soluble phenolics (Bariska and Pizzi
7 1986), thus alleviating the inhibitory effects of phenolics on soil organisms and roots. Nitrogenous
8 compounds such as ammonia, amino-acids and proteins, have also a strong chemical affinity for
9 decaying wood (Mortland and Wolcott 1965). Because decaying wood fixes atmospheric nitrogen
10 (Cornaby and Waide 1973), it can be considered as a reserve of nitrogen that increases during the
11 course of wood decomposition (Graham and Cromack 1982). Decaying wood is also a reserve for
12 water. Its high surface area and the capillary system formed by open xylem vessels create a strong
13 water-retention capacity, which increases as decomposition progresses (Käärik 1974)..

14
15 There are strong similarities between well-rotten wood and mull humus, despite their different chemical
16 composition. Both strongly adsorb water and nutrients and have a high capacity for polymerizing
17 phenolics and other organic metabolites, because of their high surface area and electronegativity.
18 Indirect evidence of properties in common between decaying wood and mull humus is the fact that the
19 widespread early-stage mycorrhizal fungus, Thelephora terrestris (Mason et al. 1983) occurs both as a
20 mycorrhizal symbiont on trees rooting in mull humus (for instance in nurseries) and as a free-living
21 saprophyte in rotting wood (Lanier et al. 1978, Bunnell et al. 1980). Thus decaying wood can be
22 considered as another kind of humus favourable to the establishment of coniferous seedlings. But
23 whereas mull humus is scarce in subalpine and boreal zones decaying wood is abundant (Sirén 1955,
24 Bernier 1996). Thus, in the long-term management of forests in severe climates, it is probably
25 desirable to maintain an abundance of large woody debris, such as dead trunks (Ponge et al. 1994).

26 27 **Scaling processes: from humus layers to ecosystem dynamics**

28
29 At first sight it may seem unrealistic to extrapolate from the scale of tiny organisms such as field- and
30 bottom-layer plant species, soil animals, and microbes, to the scale of the whole forest. However, the
31 many feed-back processes involving trees and smaller plants, animals and microbes, lead logically to

1 such synthesis. Humus layers are the seat of major processes such as plant litter decomposition,
2 nutrient and water uptake. As noted earlier, the establishment of a young tree or of a group of trees
3 may determine changes in the immediate environment (e.g. shading, soil acidification) as its branch
4 and root systems develop, and these in turn influence soil biological processes. Even though a tree is
5 subjected to a strong selection from its own environment in the first years of its life, its influence
6 becomes more and more prominent, and increases in space as its crown and root system enlarge and
7 eventually fuse with those of other individuals. Similar effects may be observed with herbaceous and
8 woody ground vegetation, especially when a single species becomes dominant and resistant (Emmer
9 1994, Bernier and Ponge 1994). In turn, humus layers built during the development of particular kinds
10 of ground vegetation or of tree stands may influence the subsequent course of forest dynamics through
11 their selective action on seedling establishment. Although these ideas were put forward a half-century
12 ago by Watt (1947) for vascular plants, they have been neglected in modelling complex ecosystem
13 dynamics and trying to understand the transition from small-scale to large-scale processes (Coleman
14 et al. 1992).

15
16 In order to understand better the transition from small-scale to large-scale processes, the time required
17 for the development of a given component of the forest should be taken into account. The colonization
18 of regeneration niches (Grubb 1977) by individuals of plant species with strong competitive and
19 phytotoxic properties may be considered as a starting point for long-term changes in the community
20 (Messier and Kimmins 1991). Similarly important event is the colonization of the humus profile by
21 individuals of species that have a strong influence on decomposition processes (such as some white-
22 rot fungi of litter) or on humus-forming processes (such as burrowing earthworm species). Colonization
23 by bracken (Pteridium aquilinum) and some heath and grass species, can lead to their spreading
24 clonally to form large patches (Watt 1956, Maubon et al. 1995), unless conditions preclude such local
25 dominance (Watt 1976, Hester et al. 1991). If such a patch appears, where the plant biomass is mostly
26 of just a single species, then a new structural unit has appeared in the ecosystem. Locally, this
27 structural unit will change environmental conditions (e.g. microclimate, humus), but nothing else may
28 happen at the level of the ecosystem except when the eventual regeneration of the forest on this patch
29 is impeded by competition, or because of the presence of a humus form unfavourable to tree seedling
30 establishment, perhaps because of phytotoxic properties. The transition to a larger scale is, again, a
31 question of repetitiveness. A patch of a clonal species may have only a temporary or small effect on a

1 limited part of the ecosystem. However, if this patch fuses with others similar in accompanying features
2 (including soil communities), then the ecosystem may change locally to the extent that it must be
3 classed as a new type (Figure 2). This has been shown in spruce (Picea abies) forests in France,
4 where the development of mor humus inside patches of Vaccinium myrtillus prevented the
5 establishment of spruce seedlings (Bernier et al. 1993, Bernier and Ponge 1994, Maubon et al. 1995).
6 In the same way post-fire dominance of crowberry (Empetrum hermaphroditum), in Sweden has been
7 shown to have long-term effects where it can lead to accumulation of mor humus and ultimately to a
8 failure of Scots pine (Pinus sylvestris) stands to regenerate themselves as illustrated by Figure 1
9 (Zackrisson et al. 1997, Wardle et al. 1997).

11 **The landscape: competition between ecosystems at the edge of the forest**

12
13 Altitudinal or latitudinal limits of forest ecosystems are generally viewed as transitions that relate the
14 presence of tree species to climatic conditions (Sirois 1992) or to the influence of human activities
15 (Zackrisson 1985). Recent research about the role of interactions between plants, animals and
16 microorganisms in ecosystem dynamics gives a more detailed picture of the processes involved in the
17 formation of the upper forest limit.

18
19 In mountain spruce (Picea abies) forests of the Alps, the establishment of spruce seedlings depends
20 on the presence of mull humus or decaying wood (Ponge et al. 1994). In either case establishment
21 occurs only when two processes are dominant in the ecosystem: the transformation of moder humus
22 to mull through the development of burrowing earthworm populations (followed by active
23 mineralization), and the decomposition of wood by fungi. We propose to name this, when
24 mineralization exceeds photosynthesis, the heterotrophic phase. In contrast, during what we call the
25 autotrophic phase, the growth of trees is characterized by carbon accumulation, increased uptake of
26 nutrients, and the development of moder humus in the topsoil, thus photosynthesis exceeds
27 mineralization. Both these phases show a de-coupling of the ion cycle of the ecosystem, i.e. are
28 departures from equilibrium (Ulrich 1986). Any process by which the autotrophic phase restricts
29 subsequent tree regeneration will degrade the forest, and in the long-term a treeless ecosystem may
30 develop (Bernier 1996). The restriction of the regeneration niche by autotrophic processes creates a
31 dynamic forest limit (Figure 3). When a severe climate limits the activity of decomposer organisms,

1 mull-forming processes may be impeded and, under even more extreme conditions, wood decay also
2 slows down. Other events such as atmospheric pollution, wide-scale deforestation, fires, or climate
3 changes, can also result in the loss of the heterotrophic phase (Zackrisson et al. 1995) and thus
4 degeneration of the forest ecosystem (Figure 1). Such degradation processes were described by Sirén
5 (1955) for boreal forests of northern Europe.

6
7 Forests may include patches of dwarf-shrub vegetation that may share several features with
8 ecosystems found above tree lines such as humus condition (Bernier and Ponge 1994) or mycorrhizal
9 systems (Read 1991). In a patchwork ecosystem, the different patches may variously interfere with one
10 another by plant-plant interactions, incompatibility between mycorrhizal systems, humus form, shading,
11 and other mechanisms, as illustrated by Figure 4. Thus the forest boundary should be viewed rather as
12 a fragmented and fluctuating limit influenced but not directly controlled by climatic conditions or
13 management.

14
15 These new ideas about the altitudinal or latitudinal limit of forests (the tree line) may have bearings
16 upon the more general concept of the ecotone (Van der Maarel 1990). An ecotone, defined as the
17 borderline between two distinct ecosystems, should be viewed as the zone in which ecosystems,
18 including soil organisms and ground flora, compete. Decreases in the competitive ability of forest
19 ecosystems, in particular in their renewal processes, may explain why changes in climate or human
20 activities may lead to profound changes difficult to reverse, such as desertification.

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23
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1 **Figure legends**

2
3 Fig. 1. The degraded boreal forest in northern Sweden. The ground vegetation is dominated by
4 cowberry (Empetrum hermaphroditum) which impedes the renewal of the native Scots pine
5 (Pinus sylvestris) forest through biochemical interactions. Cutting operations during the past
6 two centuries have favoured this degradation.

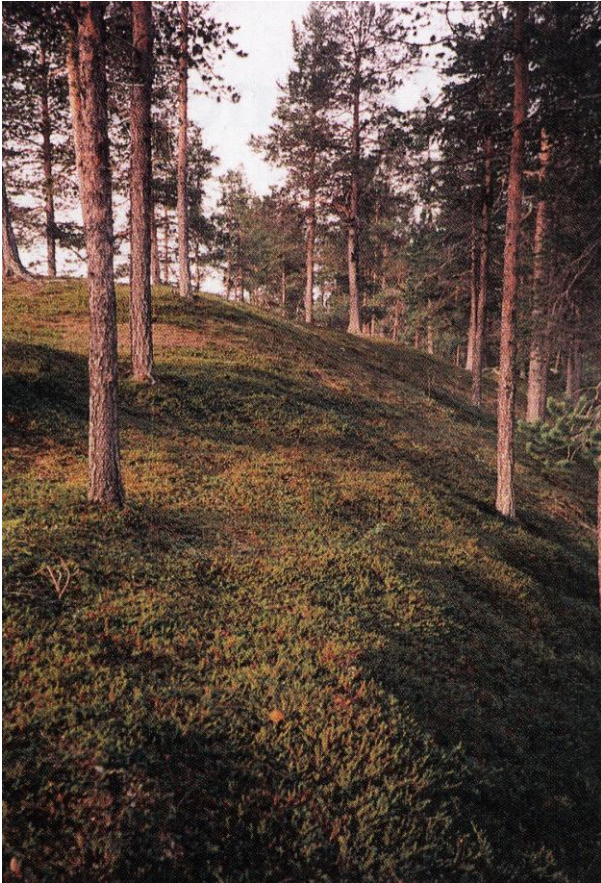
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8 Fig. 2. The transition from inter-species competition to competition between ecosystems in woody
9 areas. A = forest structural species (single or multiple); B = heath structural species with clonal
10 development; 1 to 6 = steps from A-dominated ecosystem to B-dominated ecosystem.

11
12 Fig. 3. Schematic representation of the dynamic forest limit on a northern slope (northern French Alps).
13 A = autotrophic phase; H = heterotrophic phase (see text). Hologenic faeces are faeces of
14 animals (enchytraeids, litter-dwelling earthworms, arthropods) consuming organic matter only,
15 generally distributed in a horizon underlying recognizable leaf litter horizons. Their
16 accumulation characterizes moder humus forms. Organo-mineral faeces are faeces of animals
17 (mostly soil-dwelling earthworms) consuming organo-mineral material (endogeic species) or
18 mixing organic matter to mineral matter (anecic species). Their accumulation characterizes
19 mull humus forms. Leached organic matter is made of colloidal organic particles which can be
20 leached through the soil profile and may chelate metals (podzolization). Mineral horizons are
21 mainly composed of mineral particles. They underlay the biologically active part of the humus
22 profile. Under 1000 m altitude, mull humus is dominant throughout the forest cycle, with a
23 weak accumulation of organic faeces of small animals (moder humus) during the pole phase.
24 Regeneration (of Norway spruce, silver fir) through seedling establishment after gap opening is
25 easy, whatever the size of openings. Heath patches of bilberry (Vaccinium myrtillus) occupy
26 small areas, with a thick mor humus, where regeneration is impossible. Between 1000 and
27 1800 m altitude, the forest cycle is characterized by strong changes in humus forms, with the
28 appearance of a dysmoder humus (moder with a thick layer of organic faeces) during the pole
29 phase, being progressively transformed into a dysmull (mull with imperfectly incorporated
30 organic matter) in the mature phase, then in a true earthworm mull in gap openings provided a
31 bilberry heath is not established before regeneration occurs (gaps of a sufficient size). The

1 regeneration niche (of spruce) is restricted to places with a mull humus and decaying wood
2 (multiple gaps). Bilberry heath occupies small gaps (mostly favoured at this elevation by badly-
3 adapted silvicultural practices), with a mor humus not conducive to the establishment of spruce
4 seedlings. Above 1800 m altitude, mor humus is always present, whether in coniferous thickets
5 (Norway spruce, European larch, cembro pine) or in ericaceous heath (bilberry,
6 rhododendron). Regeneration occurs through the establishment of seedlings on decaying
7 wood and through layering only at the upper forest limit.

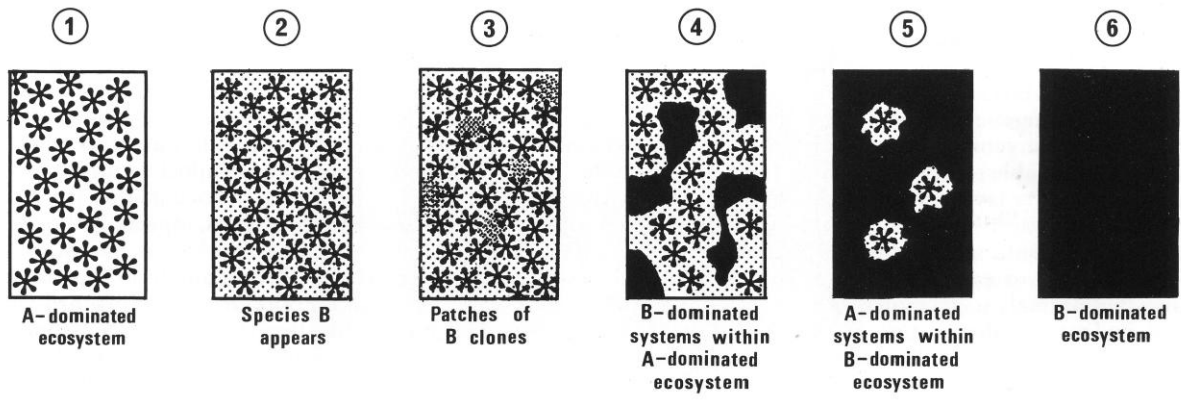
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9 Fig. 4. Diagram (a) illustrating the separation of an altitudinal gradient into space-time processes.

10 Heath competes with forest at mid elevation where both can establish themselves in similar
11 ecological conditions (gap openings, mull humus). This creates a dynamic equilibrium (inner
12 forest limit), which can be strongly influenced by silvicultural practices (cutting operations) and
13 natural disturbances (storms, avalanches). Diagram (b) showing favourable microsite
14 conditions (mull humus) for the establishment of both tree seedlings (seed rain) and bilberry
15 heath (development of subterranean parts) at mid elevation, and the fate of humus profiles
16 under forest (moder) or heath (mor) ecosystems.



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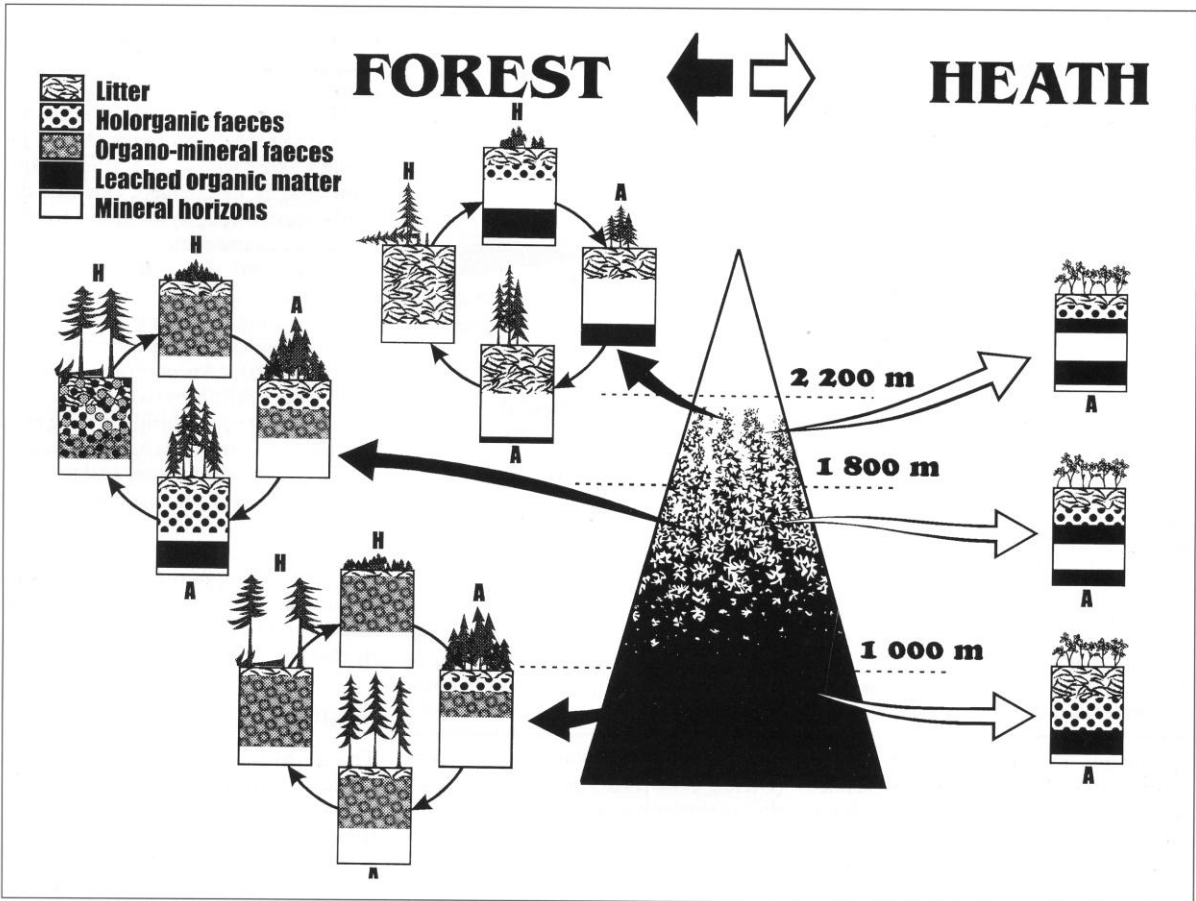
Fig. 1



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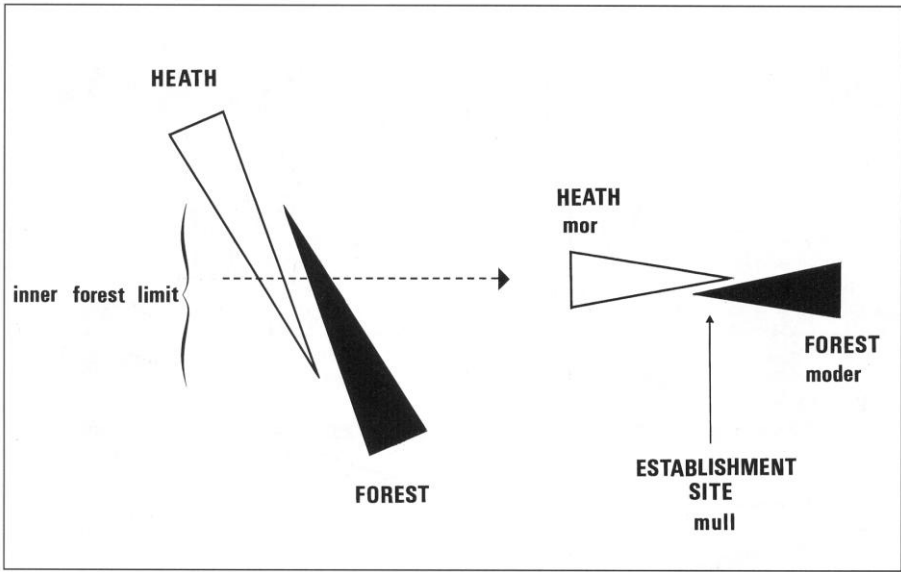


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Fig. 3

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Fig. 4