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Habitat thresholds for focal species at multiple scales and forest biodiversity conservation — dead wood as an example

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We present an example of how systematic studies of habitat loss thresholds at multiple scales can be used for assessing the functionality of habitat networks. The different steps are: (1) carefully select a suite of species representing each land cover type; (2) use quantitative targets based on the requirements of the focal species at multiple scales; (3) make regional gap analysis for the different land cover types; (4) use habitat modelling to build spatially explicit maps describing the probability that existing habitat patches really contribute to the functional connectivity of that theme in the landscape. The latter is important, since gap analyses alone neglect aspects like the quality, size, duration and configuration of land cover patches, and therefore overestimate the amount of functional habitats. The presence of thresholds at different scales suggests that the conservation management should be planned in a spatially explicit way.

Introduction

During the 1990s there has been a development in forestry towards multiple-use policies and management with less emphasis on timber production, and more on non-timber values. In Europe, the role of forests should no longer be only to sustain high wood production, but also to maintain the vitality and health of forests, biodiversity, and protective functions of ecosystems, as well as to produce non-wood resources and to support socio-economic development at multiple scales (Liaison Unit in Lisbon 1998). Being a concern on the international market place, biodiversity maintenance has become an issue, especially in countries and regions, which are dependent on exporting wood products (Elliot & Schlaepfer 2001). Hence, only about fifteen years after the term biodiversity was coined (Wilson 1985), the maintenance of biodiversity has become recognised as a central aspect of sustainable forest management.

To really succeed with the long-term maintenance of the compositional, structural and functional aspects of forest biodiversity (for definitions *see* Larsson 2001), the combined effects of protected areas, management by silviculture, traditional woodland management, as well as re-creation by planting new forests need to be assessed (Angelstam 2002). Such integrated assessments should cover whole physical landscapes (Angelstam *et al*. 2001, 2003a, Puumalainen *et al*. 2002). The reason is that in most parts of Europe 'forest biodiversity' is not the same as 'biodiversity in forests' in the traditional sense (Angelstam *et al*. 2001). Europe's forests exhibit large variation, from naturally dynamic forests to landscapes deeply modified by man. Components of forest biodiversity such as species, habitat structures and important processes are often found outside what is traditionally considered as forest. Land use systems important for forest biodiversity therefore include ancient agricultural landscapes with large single trees and hedgerows, woodland pastures, coppice, high forest, and naturally dynamic forest found in large intact wilderness areas (Kirby & Watkins 1998, Yaroshenko *et al*. 2001). A simple and practical definition of land use systems important for forest biodiversity would be "an assemblage of trees that host a variety of species and processes found in the authentic forest of the region". By "authentic" we mean landscapes with forests or woodlands, including ancient agricultural landscapes, which are still found in remote parts of Europe, as they appeared before the intensive changes that took place during the industrial and agricultural revolutions. The threats to biodiversity in all these forest environments are usually related to intensive management (e.g., Larsson 2001): (1) reducing the number of species (a compositional aspect); (2) decreasing the amount of dead wood, large trees, old and structurally diverse stands, large stands and intact areas (structural aspects); and (3) altering important ecosystem processes (functional aspects). Examples of the latter are over-browsing by deer due to the decline in large carnivores, suppression of fire, and the widespread incidence of harmful insects and fungi in monocultures. In addition, pollution and global climatic change affect forest ecosystems.

However, even if forest management practices have been recently improved to meet the new policies, the actual degree of success in maintaining different elements of biodiversity in reality is uncertain (Larsson & Danell 2001, Korpilahti & Kuuluvainen 2002). Assessing the status and trends of the components of biodiversity is therefore an important challenge, which needs to be solved to evaluate to what extent policies about biodiversity make landscapes develop in the desired direction.

Dying and dead trees, in particular, have been recognised as being of prime importance as resource and habitat for numerous animal and plant species (McComb & Lindenmayer 1999, Jonsson & Kruys 2001). Recently, the amount of dead wood has been proposed as a new indicator of forest biodiversity to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (http://www.minconf-forests.net/). Dead wood also figures in modern certification standards for best forestry practices, as defined, for example, by the Forest Stewardship Council (FSC). Nevertheless, few quantitative target values have been defined for dead wood management purposes, and they often lack well-founded scientific bases.

True assessments of biodiversity elements such as dead wood require both systematic monitoring and quantitative targets to be met. Despite the difficulties in operationalising a rigorous assessment approach, recent developments in conservation biology and landscape ecology already provide promising tools to resolve the problems of defining environmental sustainability quantitatively (Angelstam & Breuss 2001, 2003, Puumalainen *et al*. 2002). First, methods to measure the elements of biodiversity at multiple spatial scales are available in the form of data regularly collected as a part of forest management, and through specific research (e.g., Siitonen 2001). Second, operational targets for the amount of habitat required by species can be based on the non-linear responses in their occurrence and fitness along gradients of habitat change at multiple spatial scales (Jansson & Angelstam 1999, Carlson 2000, Muradian 2001, Fahrig 2001, Angelstam & Breuss 2001, 2003).

The aim of this paper is to provide an example of how systematic use of the appearing concepts of focal and umbrella species representing different forest environments (Roberge & Angelstam 2003) and habitat loss thresholds at multiple scales including patch quality, size, duration and context can be used for assessing the functionality of habitat networks. We also discuss how this approach can improve the implementation of policies on biodiversity maintenance.

Habitat thresholds at multiple scales

Focal forests and species

The loss of species richness associated with systematic habitat loss over time can be viewed as a dramatic journey where species with different life-history traits pass through a series of thresholds representing the levels of communities, populations and individuals. To detect a response of habitat loss in living organisms, it is necessary to identify the appropriate spatial and temporal scale at which a particular species responds (Lord & Norton 1990, Wiens 1995). Species most sensitive to habitat fragmentation and loss are usually those that: (1) have large area requirements (Wilcox 1980), (2) are sedentary specialists (Opdam 1990), (3) occupy late successional stages (Gotelli & Graves 1990), and (4) have a low dispersal ability (Pimm *et al.* 1988, Bolger *et al.* 1991).

The boreal forest is characterised by a wide variety of disturbance regimes and forest types, each of which harbour different suites of species. Maintaining viable populations of all naturally occurring species thus requires that several complementary functional habitat networks be maintained, and the problem of fragmentation and loss must be dealt with for each of the different forest environments at multiple scales (Angelstam 1998, Angelstam & Andersson 2001). The focal-species approach (*sensu* Lambeck 1997) provides a systematic framework for the planning of such habitat networks in time and space. This approach is consistent with the concept of umbrella species (e.g., Fleishman *et al.* 2000, Caro 2003), defined as species whose conservation contributes to the protection of numerous naturally co-occurring species. Focal species are selected among the most demanding species regarding some resources or processes (e.g. Lambeck 1999). Their 'umbrella' function is based on the theoretical assumption that providing habitats in right quantities and qualities for the most demanding species will also fulfil the needs of all other species dependent on the same habitats. By using the requirements of carefully selected focal species for each forest type of conservation interest, it would be possible to derive quantitative targets for a range of biodiversity components (Roberge & Angelstam 2003).

For example, Mikusiński *et al.* (2001) showed that the presence of the three-toed woodpecker (*Picoides tridactylus*) and the white-backed woodpecker (*Dendrocopos leucotos*) is associated with a high species richness of other forest birds. Their habitat specialisation suggests that these two species could be used as indicator species for authentic coniferous and deciduous forests, respectively (Martikainen *et al.* 1998, Angelstam *et al.* 2002). Moreover, based on a good understanding of what resources these species require, and on the appearing knowledge about how much they need at multiple spatial and temporal scales for maintaining viable populations, they have potential for being used as focal species for the planning of networks of old forest with natural dynamics. Dead wood of different types appears to be the critical resource for these two focal species.

Dead wood thresholds for patch occupancy

For spruce-dominated forests, Bütler *et al.* (2003a, 2003b) developed targets for standing dying and dead trees at the scale of habitat patches. This was based on the quantitative habitat requirements of the three-toed woodpecker, whose presence was considered an indicator of the properties of naturally dynamic spruce-dominated forests. First they developed a theoretical model based on energy requirements predicting probabilities of woodpecker presence as a function of available snag quantities. Then an empirical field study was conducted in subalpine spruce (*Picea abies*) forests in Switzerland with the aim of verifying the model predictions. For this purpose, 12 pairs of sites of one km^2, each comprising one site with and one without breeding three-toed woodpecker were sampled for snags. Finally, the comparison of the theoretical model with the empirical data enabled the derivation of quantitative snag targets for spruce forests.

Both the theoretical model and the logistic regression analysis of the empirical data resulted in similar estimates of the minimum snag quantities for woodpecker occurrence. For management purposes, Bütler *et al*. (2003a) argued for the precautionary principle by striving for target values of 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) or 14 (diameter at breast height ≥ 21 cm) snags per hectare in an area of 100 ha. A probability of ≥ 0.9 for woodpecker occurrence was applied in both approaches. In another study, Bütler *et al*. (2003b) compared the habitat occupancy threshold for the amount of dead wood in the Swiss study mentioned above with that in boreal forests of south-central Sweden. The probability of three-toed woodpecker occupancy increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m^2 ha^{-1} in Switzerland and from 0.3 to 0.5 m^2 ha^{-1} in central Sweden. The present amount of dead wood in managed landscapes is currently 10%–20% of these target values (Siitonen 2001). In Sweden a political target for increasing the amount of dead wood with 25% until 2010 has been formulated (SOU 2000: p. 480). To be cost-effective, the research on this focal species suggests that in contrast to the current management paradigm where nature considerations are dispersed rather evenly over whole landscapes, future forest management should aim at concentrating dead wood in the form of a network of at least 100-ha forest patches in which the ecological dead wood target is reached.

In hemiboreal forest, Angelstam *et al*. (2002) evaluated the relationships between dead wood variables and the presence of different woodpecker species in five different coarse landscape types in NE Poland. These ranged from reference areas for forest biodiversity in the region in the Białowieża National Park, forests with two different management intensities, plantations on former agricultural land, and to natural forest succession after land abandonment. In each of these five coarse landscape types, they used playback of drummings to survey woodpeckers in a total of 25 one-km^2 plots during the pre-breeding period in early spring. The mean number of woodpecker species per km^2 varied from 0.6 (plantations) to 4.8 (Białowieża National Park). While the generalists (black woodpecker *Dryocopus martius* and great spotted woodpecker *Dendrocopos major*) were found in all five coarse landscape types, the specialists (lesser spotted woodpecker *D. minor*, white-backed woodpecker, middle spotted woodpecker *D. medius*, grey-headed woodpecker *Picus canus* and three-toed woodpecker) were observed only in landscape types without intensive forest management and in natural forest succession after land abandonment. Of the habitat structures measured, the amount of dead wood and large deciduous trees with large dead branches were closely correlated with the presence of the specialised woodpecker species.

For the most area-demanding deciduous forest specialist, the white-backed woodpecker, there was a clear non-linear relationship between the amount of dead wood and the species' presence. The required volume of deciduous dead wood was estimated to between 10 and 20 m^3 of dead wood per hectare over a 100-ha area. An interesting observation was that the amount of deciduous dead wood and white-backed woodpecker incidence was similar in the natural succession after abandonment of wooded mead-

Table 1. Amount of standing dead wood (m^3 ha^{-1}) in patches with indications of breeding three-toed (Bütler *et al.* 2003a, 2003b) and white-backed woodpeckers (Angelstam *et al.* 2002).

	Unsustainable	Uncertain	Sustainable	Reference area
Three-toed woodpecker	< 7	7–18	≥ 18	Swiss sub-alpine forest
White-backed woodpecker	< 10	10–20	≥ 20	Białowieża National Park

ows and pastures as in the Białowieża National Park used as a reference area. Although clear relationships were observed, this study contains presence/absence data from one field season only and it did not include any fitness measures. Therefore, to improve estimates of the quantity and quality of dead wood required, bird-habitat relationships need to be explored in more detail.

The studies of these two potential focal species with an apparent umbrella function suggest that the threshold values for both deciduous and coniferous snags at the scale of habitat patches were 5–10 times more than the volume found in a managed forest in Fennoscandia and about a fifth of what is found in naturally dynamic forest (cf. Siitonen 2001). Table 1 summarises the threshold values for dead wood for these two species.

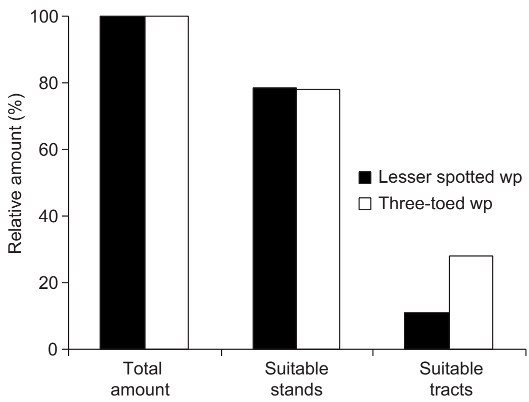

Fig. 1. Illustration of how regional gap analysis overestimates the amount of functional habitat for individuals (suitable stands) and local populations (suitable tracts) in forest found in the counties Dalarna and Gävleborg covering 55 000 km^2. Total amount is defined as the total amount of habitat currently present according to the regional gap analysis (*see* Angelstam *et al.* 2003a).

Habitat models as a tool to evaluate the functionality of habitat networks

To evaluate the extent to which existing networks of patches of different forest types are functional there is a need to develop procedures for assessing networks of conservation areas, and subsequently use that as a basis for planning conservation and restoration measures. There is a multitude of factors affecting the distribution and abundance of a species. For operational spatially explicit planning purposes, however, some simplification is necessary. Habitat suitability index (HSI) modelling consists of combining spatially explicit land cover data with quantitative knowledge about the requirements of specialised species and building spatially explicit maps describing the probability that a species is found in a landscape (Verner *et al.* 1986, Scott *et al.* 2002). With adequate quantitative data on a suite of particular focal species, a series of predictive landscape models for the different vegetation types in a landscape can be built. This requires quantitative information on the habitat requirements of the species on at least three spatial scales: viz. stand quality, stand size and landscape configuration, as well as the rate of habitat renewal (Angelstam *et al.* 2003b).

Using a land cover map based on satellite images with different forest environments and site types, and habitat thresholds at the scale of patches and local landscapes, thematic maps showing tracts with suitable habitat for different focal species were made for a 55 000 km^2 area in central Sweden (Angelstam *et al.* 2003a). The selection of focal species was based on a regional gap analysis (op. cit.). This suite of species included specialised birds, a beetle, and lichens dependent on a humid micro-climate. A Geographic Information System (GIS) and parameters for the requirements of the selected focal species at different spatial scales corresponding to the levels of individuals and populations were then employed to produce HSI maps.

The HSI-modelling procedure can thus be described as a gradual elimination of unsuitable patches of a particular focal forest type in the digital data base until only sufficiently large and connected patches (from the target species' point-of-view) remain. Using the different steps in the HSI-modelling procedure Angelstam *et al.* (2003a) compared the amount of the focal forest types considered important in the regional gap analysis with the amount of forest patches, which can be considered as fully functional to maintain viable local populations in the short term. For the seven species used as potential focal species for coniferous and deciduous forest, the average maximum level of overestimation was about 5-fold (*see* Fig. 1 for two examples).

Discussion

Gap analyses overestimate the functional amount of habitat

Any regional gap analysis based solely on the amount of different land cover types will overestimate the amount of functional habitat. If, for example, a given amount of habitat is subdivided into many small and isolated patches, the function of the habitat network will be different as opposed to if the patches are large and close to each other. Mykrä *et al.* (2000) showed that in Finnish boreal forest, a long history of forest management has resulted in a very truncated range of patch sizes compared with naturally dynamic landscapes. A major determinant of such landscape patterns is the type of ownership and the associated management regimes of the landscape.

The work with regional gap analysis and HSI-modelling in central Sweden's boreal forest suggests that due to thresholds at the scale of stands and landscapes, only one fifth of the areas present as assets in the regional gap analysis may actually be located in tracts, where patches are sufficiently large and well-connected. Two additional sources of overestimation, which need to be evaluated, are the internal quality of the stands and the need for habitat renewal depending on the longevity of patches. The research on dead wood thresholds suggest that, to ensure functionality for the focal species, forest management should be planned so that the set-aside of trees and stands are made in a way that concentrates both dead wood in stands and suitable stands with high dead wood amounts in landscapes. This is in stark contrast to the generally applied biodiversity management practice where general considerations are made in a similar way throughout the landscape.

Another aspect that affects biodiversity assessment is time delays in population response as habitat is destroyed (Tilman *et al.* 1994, Hanski & Ovaskainen 2002). This is implicit in the relaxation concept from island biogeographic theory and means that sub-populations may persist for some time in a landscape below the habitat threshold (*see* Carlson 2000). Hanski (1998) calls them 'living dead' populations and species. The time delay is expected to be especially long if the species is located close to its extinction threshold following habitat loss and fragmentation. Therefore we have to be careful with threshold values for dead wood values obtained from deeply modified forest landscapes (e.g. south-central Sweden), even if some three-toed woodpeckers still persist.

But how large should the size of a landscape planning unit be? Angelstam *et al.* (2003b) used information about habitat patch quality, size, duration and context from 17 specialised potential focal forest bird species to estimate the tentative size of planning units for the assessment of habitat networks aimed at maintaining biodiversity. The estimated mean minimum size of planning units ranged from 40 000 to 250 000 ha, depending on the assumptions. By contrast, the size of individual conservation areas such as woodland key biotopes and protected reserves from which habitat network can be built in a managed matrix was 1–1000 ha. Therefore, when managing for the maintenance of forest biodiversity there is a need to extend the spatial and temporal scale from the stand scale to that of landscapes within large management units.

Conservation science is sometimes like advocacy. Different specialists work with different species representing different forest types and spatial scales. The examples of potential focal bird species discussed above are based on the precautionary principle that providing enough for area-demanding species will benefit many other species. However, other taxa dependent on other aspects of dead wood may have other requirements related to the size, stage of decay and amount of dead wood (Jonsson & Kruys 2001). For example, the occurrence of different species of saproxylic beetles in boreal forests is closely linked to the types and amounts of decaying fungi (Kaila *et al.* 1994, Wikars 2003). Similarly, the small-scale distribution of many non-vascular plants is influenced by micro-climatic conditions that are not directly relevant to bird habitat choice. Therefore, the selection of suites of focal species for the management of forest biodiversity must consider these differences.

In spite of its complexity, dead wood is only one of the structural elements in a forest. The systematic approach, which we advocate, should also be pursued also for other habitat elements in different forest environments (Angelstam 1998, Nilsson *et al*. 2001). The concept of natural forest disturbance regimes provides a blueprint for the kinds of forest environments and structural elements for which targets ought to be developed (e.g. Korpilahti & Kuuluvainen 2002). Based on the threats to the population viability of forest specialists, sun-exposed dead wood, large trees, deciduous trees, wet old-growth, recently burned forests and ancient woodland are examples of other forest elements where a systematic approach to derive ecological targets for occurrence, populations viability, ecosystem integrity and even resilience should be encouraged.

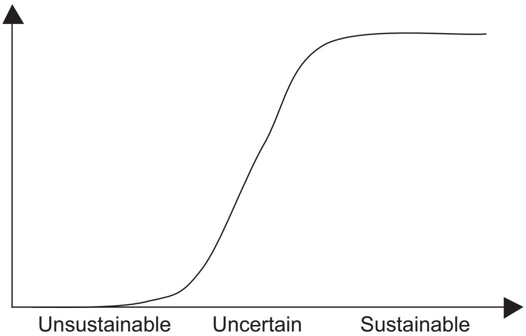

Fig. 2. Instead of looking for particular threshold values, we suggest that non-linear relationships should be viewed as having three intervals: unsustainable, meaning that the amount of the particular resource is well below the uncertain interval; sustainable means the amount is well over this part of the gradient in the resource; and finally uncertain.

Sustainable landscapes — research on targets for biodiversity

Being authentic ecosystems in most of Europe, and a renewable resource from which socio-economical wealth can be generated, both forest and woodland represent landscape types of paramount importance for sustainable development. In order to ensure sustainable development, criteria and indicators to measure the progress must be combined with targets allowing assessment of the degree to which sustainability has been achieved. Developing ecologically founded targets for other focal forests and species is an important task for ecologists. We argue that the components of biodiversity are excellent proxy measures for the evaluation of the environmental aspect of sustainable development in landscapes.

Goodland and Daly (1996) described four degrees of environmental sustainability: weak, intermediate, strong, and absurdly strong sustainability. Weak sustainability means "maintaining total capital intact without regard to its composition from among the four different kinds of capital", and assumes that different kinds of capital are perfect substitutes. The concept of strong sustainability requires maintaining different kinds of capital intact separately. It assumes that natural capital and human-made capital are not substitutes but rather complements in most production functions. The appearing knowledge about ecological thresholds (Muradian 2001) suggests that strong, or at least intermediate sustainability should be the goal. The full functioning of the socio-environmental system thus requires separate assessments of the different kinds of capital. Thresholds for occupancy and population viability in relation to patch quality, size, duration and context in a landscape need therefore to be linked to the discussion on sustainability. However, rather than looking for exact habitat threshold values, we argue that the main criteria for establishing targets should be to identify the ranges of values that define clearly insufficient, uncertain and clearly sufficient amounts of the resource (Liu & Taylor 2002) (Fig. 2).

The success in facilitating sustainable development of landscapes is also largely dependent on the initial conditions. Due to differences in the historical development in Europe, the land use patterns in the West and the East differ substantially (Angelstam *et al*. 1997). The industrial revolution and the associated intensified habitat alteration spread from the western to the eastern part of continental Europe during the 19th century (Chirot 1989). In the West, wood production has been high and intensive for a long time, and biological diversity has suffered. Hence, because of a long and intensive land use history, landscapes in the western part of the Baltic Sea region contain a "narrowed" range of forest environments as compared with pre-industrial conditions. In the East forestry was less intensive, and the existing remnants of the original biodiversity are still relatively abundant. By contrast, in Western Europe forest plantations, if well planned and with sufficient structural quality, could in the long-term improve and restore the functional connectivity (Mikusiński & Angelstam 2001).

Therefore, we suggest that method development and subsequent assessment of intermediate or strong sustainability should be attempted in replicated physical landscapes spanning the variation in forests and woodland in Europe's main ecoregions from severely altered landscapes in the West to relatively intact landscapes in the East. Hence, one could use past history of management in different landscapes of the Baltic Sea region as a large-scale mensurative experiment (*sensu* Krebs 1999), where the requirements of demanding species in terms of dead wood and other structural components of biodiversity could be measured and compared. More generally, such a network of case studies could become the basis for integrating assessments of environmental, social, and economic sustainability.

Implementing targets for biodiversity conservation

Scientific knowledge from the field of natural sciences about thresholds and derived targets for environmentally sustainable development will not be sufficient for successful maintenance of biodiversity where it still exists, such as in the eastern part of the Baltic Sea region. Over the last decade, the forest sector in former Soviet Union countries with economies in transition has experienced dramatic changes (Lazdinis 2002). From the planning system in the former Soviet/socialistic system, foresters have had to adapt to operating in active market conditions with immediate decision making and a heavy load of responsibility. The absence of economic incentives to increase the exploitation of forests has now changed into high national expectations for timber exploitation, strong competition on international timber markets, reduction of staff, and hundreds of thousands of private forest owners with very small forest holdings. Control of forestry activities in some countries is not always sufficient and effective. While this development is a potential threat to biodiversity in the future, the low forest harvesting intensity in the former socialistic economies was advantageous for biodiversity. In the western part of the Baltic Sea region the challenge is to restore and even re-create different elements of biodiversity such as dead wood.

Failure to maintain biodiversity may not be just gaps in the spatial representation of different ecosystems. Institutional obstacles, usually called political and institutional failures (Mayers & Bass 1998), may also play a large role for the maintenance of biodiversity in practise. Extending this approach into the context of the forest sector in general, we also need tools for the evaluation of sustainable forest development implementation on the political level, i.e. institutional gap analysis.

Institutional gap analysis, like its ecological counterpart, can be useful not only for identification of gaps in political settings. This framework can also serve as a basis for monitoring and evaluating changes in development at both fine and coarse administrational scales. The failures in policy process (e.g., for forest policy structure *see* Worrell (1970) and Merlo & Paveri (1997)) may occur at any of the stages of implementation and also be the result of attitudes, values, and hidden objectives of those in charge (Mayers & Bass 1998, Larsen *et al*. 2000). Therefore, to facilitate sustainable development of forest landscapes, knowledge produced by natural sciences should be complemented with the expertise representing the socio-economic dimension both in education (Hammer & Söderqvist 2001) and practise (Vogt *et al*. 2002).

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