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MACROECOLOGICAL RESEARCH IN BOREAL FOREST REVEALS THE EFFECTS OF MOOSE ON ECONOMICALLY AND ECOLOGICALLY IMPORTANT TREE SPECIES*

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How to manage the impact of a large moose population on the economically important Scots pine, and on ecologically important mature aspen, rowan and willow trees as habitat for lichen, moss, insect and bird species, are hot topics in Fennoscandia for forest and wildlife managers. To understand if the study design affects conclusions about the impact of moose browsing damage on young trees of economic and ecological importance we used three macroecological approaches: (1) a comparison of Swedish forest landscapes managed for intensive coniferous wood production, (2) a natural experiment approach that compared forests with different abundance of moose in Sweden, and (3) a comparison of browsing damage across six countries in northern Europe from Norway in the west to Russia in the east. The results show that Sweden had high moose densities across all landscapes studied, high overall rates of browsing damage, and therefore a weak relationship between moose density and browsing damages. A comparison between managed forest landscapes and urban forest areas, which are less accessible to moose, showed a clear effect of moose density on tree damage of both economically and ecologically important tree species. Finally, across 10 landscapes in Sweden, Norway, Finland, Latvia, Belarus and Russia we found that moose had a strong effect on damage to both groups of tree species. Research design affects the conclusions about the role of moose density for browsing damage on economically and ecologically valuable tree species. Macroecological studies in landscapes, representing different contexts on the European continent's West and East, form a valuable approach to produce new knowledge. We discuss the need for integration of the management of moose and their predators (including man) as well as forest management and biodiversity conservation planning.

Keywords: boreal forest, moose, biodiversity conservation, forest landscape management, green infrastructure, landscape restoration, macroecology, spatial planning trophic interactions.

Sustainable forest management (SFM) policy aims at satisfying economic, ecological and social pillars of sustainability. Implementing this is not straightforward

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because different actors focus on different benefits, and often have different perspectives, knowledge and power. Seemingly simple matters may actually turn out to be complex with many interacting factors. Forest landscapes with different land use histories provide opportunity to produce new knowledge about trade-offs between different SFM dimensions in an innovative manner [3]. The term macroecology captures this [9]. Using this approach, Angelstam et al. [5] and Naumov et al. [15] demonstrate that economic and ecological benefits of forest landscapes are negatively related to each other along the gradient from short to long histories of management towards forestry intensification in the Baltic Sea Region and NW Russia. Similarly, it has been shown [11, 13] that legacies of societal steering affect the regionally desired styles of governance. Such comparative studies illustrate the opportunity of learning about how to accommodate all SFM dimensions, and to deal with trade-offs among them [20] through governance, planning and management of entire landscapes as coupled social and ecological systems [16].

The long history of use and gradual transformation of Fennoscandia's forest landscapes has led to high and effective wood production of high economic value, but also loss of natural forest properties as old deciduous trees of ecological value [5, 15]. Additionally, modification of ecosystem processes such as reduction of fire and flooding, and the presence of a large herbivore population makes restoration of naturally occurring tree species preferred by moose as food difficult, but also wood production based on tree species preferred by moose (*Alces alces*). The impact of moose to economically (Scots pine (*Pinus sylvestris*)) and ecologically important tree species preferred by moose (aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), willow (*Salix* sp.) and oak (*Quercus robur*)) is a good example. The mechanism is as follows: forest using clear-felling systems and large herbivore management actions, as well as loss of large carnivores such as wolf and brown bear, lead to increased population densities of large herbivores such as moose. This may lead to subsequent cascading effects on species, habitats and processes in forest landscapes. Therefore, the interactions among trees, large herbivores and large carnivores need to be understood [17, 18, 19].

However, the spatial extent of trophic interactions between large carnivores and herbivores, and herbivores and tree species, is very large. This makes it challenging to study because there is a risk that the research design used to study the effects of moose on tree species may affect the conclusions. This issue can be addressed by comparative macroecological studies at different spatial scales. This stresses the need to include both regions with intact large carnivore assemblages, and regions where they are no longer present, or occur in low densities. A good example of this are boreal forest landscapes on the European continent, from southern Fennoscandia in the West, where all large carnivore species are extinct or occur at low densities, to regions in NW Russia in the East, where viable populations of all four naturally occurring large carnivores (brown bear (*Ursus arctos*), wolf (*Canis lupus*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*)) are present.

The aim of this study is two-fold. First we compare three research designs to measure moose damage on the economic value of Scots pine and the ecological value of aspen, rowan and sallow. To do that we review two recent studies that (a) compare different managed forest landscapes, as well as managed forest landscapes and urban forests [6], and one (b) that compared ten forest landscapes in Sweden, Norway, Finland, Latvia, Belarus and Russia [4]. Second, we discuss management implications in terms of the need to integrate forest, biodiversity and wildlife planning and management, and how that could be achieved.

Research Methodology

Determining the size and location of study areas. Any research question requires the identification of the relevant spatial scale to address it. While trees have very small area requirements, large herbivores have large area requirements, and their predators' even larger ones. To encompass a population of moose it has been reported that in Sweden [14], moose management units should exceed from 500 km^2 in the south to 1000 km^2 in the north. Large carnivore management takes place at a regional level, exceeding one order of magnitude larger areas compared to optimal moose management area size. However, because within any particular country, management of large herbivores and carnivores are governed by similar or identical policies and management approaches, predator – prey – vegetation relationships have limited variation among landscapes and regions. On the contrary, by including several countries in the northern part of the European continent, large variation in both large herbivore and carnivore abundance, as well as forest management history and intensity, is achieved (Fig. 1).

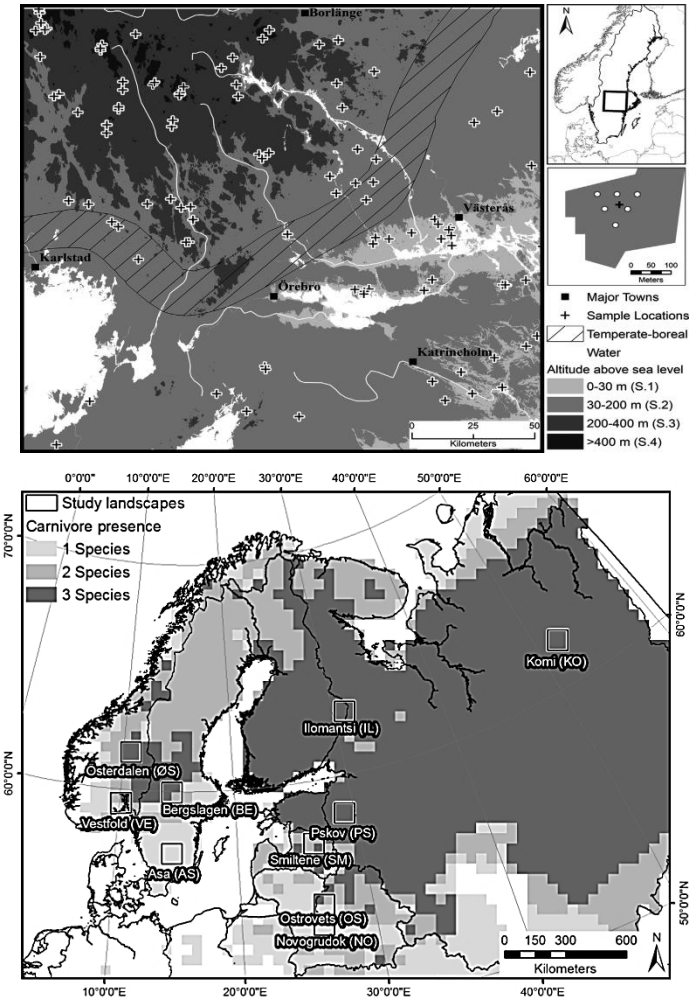

Fig. 1. Three study designs: (a) comparison of forest landscapes made in south-central Sweden at ca. 58.5°–60.5° N within four altitudinal strata, and (b) in forest stands in towns and villages (left map); (c) sam pling in a total of 10 forest landscapes in Norway, Sweden, Finland, Latvia, Belarus and Russia (right map)

Three macroecological approaches. *Managed forest landscapes in Sweden.* First, we sampled six plots in each of 120 young forest stands in the distinct temperate-boreal forest gradient in Mälardalen and Bergslagen in south-central Sweden (Fig. 1). The potential for aspen, rowan, willow and oak saplings to become recruited into the population of ecologically mature trees forming habitat of importance for biodiversity conservation, and for Scots pine to deliver undamaged saw logs was estimated. Sampling was made in forest stands representing managed forest landscapes accessible to large herbivores, dominated by moose, contributing 93 % to the total abundance of large herbivores [4, 6].

Forests with different moose access in Sweden. Next, a natural experiment approach was applied by comparing the results from sampling in young forest stands in managed forests accessible to moose, and as a control in settlements that were typically avoided by large herbivores [6].

Macroecological study in six countries in northern Europe. Finally, again using the same methodology as above, we employed a macroecological approach based on studies in each of 100 forest stands in 10 boreal forest landscapes in the Baltic Sea region and Russia (Fig. 1, right [6]). This gradient ranged from extinct to extant populations of both large carnivores and large herbivores, and from high to low forest management intensity.

Results and Discussion

Review of three approaches. Managed forest landscapes in Sweden. For rowan, willow and oak, but not aspen, we found a positive relationship between browsing damage levels and moose abundance. This may be related to high selection preference of moose towards aspen in combination with low aspen occurrence in young managed forest.

Forests with different access of moose in Sweden. Using the same sampling methodology, we found that both the focal deciduous tree species, and Scots pine, had lower damage levels in towns and villages (with limited access to moose) compared to forest sites (Fig. 2 with aspen as example). Rowan, willow, oak and Scots pine showed the same general pattern [6].

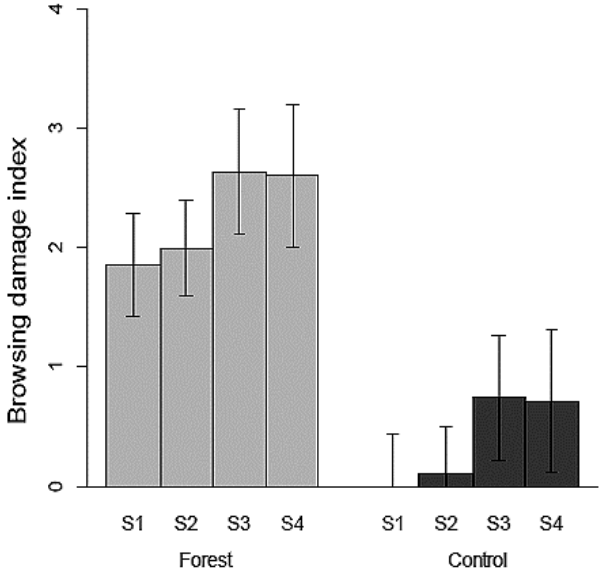

Fig. 2. Estimates of mean browsing damage level ± 95 % confidence interval for aspen (on a scale from 0 (unbrowsed) to 4 (every long shoot browsed) per plot, in four forest and control strata S1 (< 30 m a.s.l.), S2 (30 < 200 m a.s.l.), S3 (200 < 400 m a.s.l.) and S4 (> 400 m a.s.l.)

Macroecological study in six countries in northern Europe. A long history of human-induced factors made large carnivore species go extinct in the south-western part of the study area ranging from Norway and Sweden to Finland, Latvia, Belarus and Russia [4]. There was an inverse relationship between the numbers of large carnivores and large herbivores. This coincided with a steep gradient in browsing damage on the ecologically important aspen as hosts for specialised species, as well as the economically important Scots pine. In one landscape (in Norway), hunting had replaced the function of predation by large carnivores. Mean damage levels of all tree species were correlated with large herbivore abundance ($r = 0.80$, $p < 0.05$; see Fig. 3).

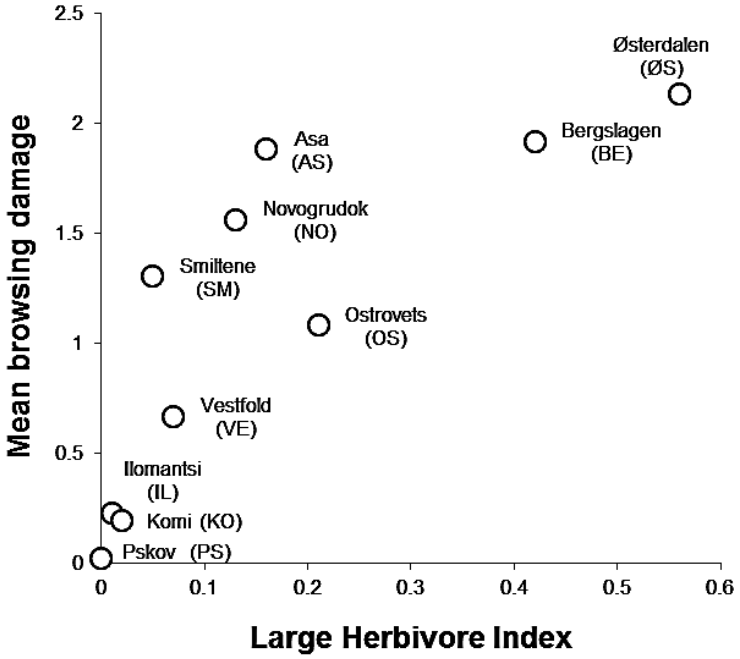

Fig. 3. Relationship between the abundance of large herbivores (using an index combining density and body weight [4]) and mean browsing damage on aspen, willow tree and Scots pine in 10 study areas in Norway, Sweden, Finland, Latvia, Belarus and Russia

Adding results from eight landscapes sampled in the same way [7] yields a sample size of 18 and a correlation coefficient of 0.74 ($p < 0.001$). There was no relationship between moose damage and forest management intensity.

Research design matters. The browsing damage index used in our studies ranged from 0 (not browsed), over 1 (< 50 % of long shoots damaged) and 2 (> 50 % of all long shoots damaged) to 3 (all long shoots damaged) and 4 (all long shoots dead). Comparing different forest stands in south-central Sweden yielded a variation in browsing damages, which is only 24 % of the variation observed in northern Europe from Norway to Russia. The comparison between forest landscapes and urban forests was intermediate (Fig. 4).

Our studies [4, 6, 7] demonstrate that research design is a crucial aspect to consider when drawing conclusion about the impact large herbivores have on ecologically and economically important tree species.

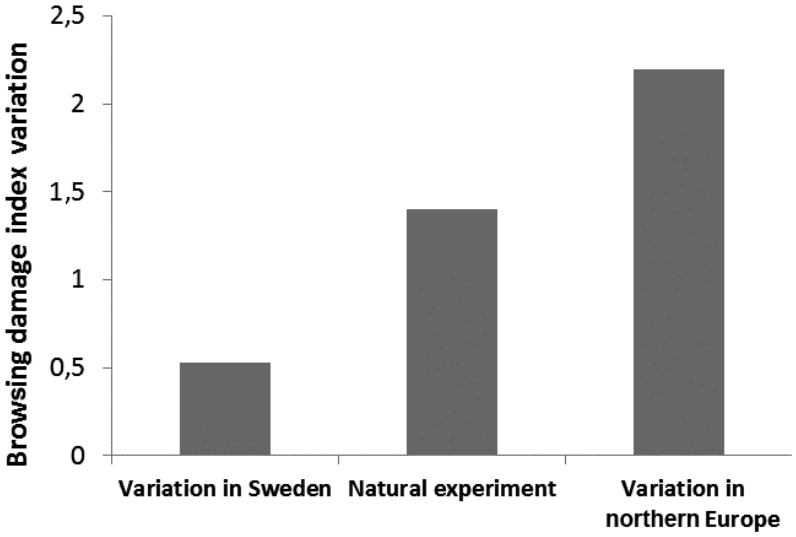

Fig. 4. Illustration showing that the design of studies of the impact on moose browsing damages on economically and ecologically important tree species affects conclusions for management (While studies in Swedish managed landscapes have small variation in moose density and tree browsing damages because they are always high, the natural experiment approach and use of variation in northern Europe shows clear relationships between moose density and tree browsing damages.)

Depending on what aspect of our research one quotes, it is possible to draw very different conclusions about the role of moose browsing damages on young trees. We conclude that comparative studies that encompass the full range of variability in moose density in northern Europe are necessary, and can enlighten the debate on how to cope with moose damage on ecologically and ecologically important tree species in Fennoscandia.

Other studies have also documented clear relationships between moose density and damage levels to young trees. In northern New Hampshire, USA, a direct correlation between browse damage and moose density was found [8]. Similarly, in Russia, Abaturov and Smirnov [1] showed that normal stand development occurred at 0.2–0.3 moose/km^2 while 0.3–0.5 moose/km^2 was associated with impaired growth of preferred forage species such as aspen. Fennoscandian moose densities are well above that level. The low abundance of preferred deciduous browse species [7], caused by a long history of forest management focus on coniferous tree species, aggravates the difficulty to reduce browsing damages on economically and ecologically important tree species.

Management Implication

Restore deciduous forest habitat networks in urban contexts. Given the difficulty to reduce browsing damage to allow restoration of mature aspen, rowan and willow trees in for example Sweden, other solutions need to be sought. With browsing damage being much lower near and in towns and villages compared to the surrounding managed forest landscapes, opportunities exist for restoration of deciduous forests' functional habitat network. However, this means that spatial planning is essential to secure that sufficient amounts of deciduous forest areas are present. This means that collaboration between county administrations, municipalities and

forest planners must be encouraged. Unfortunately, however, cross-sector collaboration between public and private sectors is poor [2, 12].

Governance and management of trophic interactions. To support knowledge production about how to encourage integrated management of large carnivores, large herbivores and cascading effects on forest ecosystems and their ecosystem services, as well as forest and conservation planning, we encourage researchers to carry out macroecological comparative studies that include variation in both landscape history, and different governance and management regimes. Future research should thus turn the sole focus from the ecology of large herbivore-forest systems towards human and societal aspect of how to best govern and manage these systems. Landscape approach builds on knowledge production and learning about and within social-ecological systems [3, 10]. The variation among countries in the Baltic Sea Region and NW Russia is a great asset for this. The knowledge generated through macroecological studies provides opportunity for initiating a process of collaborative learning among actors and stakeholders with different portfolios of landscape benefits.

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МАКРОЭКОЛОГИЧЕСКИЕ ИССЛЕДОВАНИЯ В БОРЕАЛЬНОМ ЛЕСУ: ВЫЯВЛЕНИЕ ВЛИЯНИЯ ПОПУЛЯЦИИ ЛОСЕЙ НА ЭКОНОМИЧЕСКИ И ЭКОЛОГИЧЕСКИ ЗНАЧИМЫЕ ПОРОДЫ ДРЕВОСТОЕВ

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Управление воздействием большой популяции лосей на экономически важные древостои сосны обыкновенной и экологически значимые спелые насаждения осины, рябины

Для цитирования: Ангельстам П., Педерсен С., Мантон М. Макроэкологические исследования в бореальном лесу: выявление влияния популяции лосей на экономически и экологически значимые породы древостоев // Лесн. журн. 2018. № 4. С. 9–18. (Изв. высш. учеб. заведений). DOI: 10.17238/issn0536-1036.2018.4.9

и ивы – среду обитания лишайников, мхов и птиц – является актуальной проблемой для работников лесного хозяйства и охраны живой природы в исторической области Фенноскандия. План исследования, позволяющего сделать выводы о влиянии ущерба от обгладывания лосями подроста на древостои, имеющие экономическую и экологическую ценность, основан на трех макроэкологических подходах: (1) – сравнение шведских лесных ландшафтов, используемых для интенсивного воспроизводства хвойной древесины; (2) – эксперимент в естественных условиях по сравнению участков лесов Швеции с разной численностью лосей; (3) – сопоставление ущерба от обгладывания деревьев на территории шести стран Северной Европы (от Норвегии на западе до России на востоке). Результаты исследования в Швеции выявили высокую плотность популяций лосей на всех изученных территориях при повсеместном высоком уровне ущерба и, как следствие, слабую связь между этими факторами. Сравнение эксплуатационных лесов и пригородных лесных участков, где доступ лосей ограничен, показало явную зависимость числа поврежденных деревьев экономически и экологически значимых пород от численности лосей. В заключение установлено существенное влияние численности лосей на количество поврежденных деревьев обеих групп пород на всех 10 опытных площадях в Швеции, Норвегии, Финляндии, Латвии, Белоруссии и России. Исследование дает основания для выводов о влиянии плотности популяций лосей на степень ущерба от обгладывания деревьев экономически и экологически значимых пород. Макроэкологические исследования на разнообразных участках лесов запада и востока Европы позволяют сформировать содержательный подход к приобретению новых знаний. Авторы обсуждают необходимость интеграции управления численностью лосей и их природных противников (включая человека) с управлением лесами и планированием сохранения биоразнообразия.

Ключевые слова: бореальный лес, лось, сохранение биоразнообразия, управление лесным ландшафтом, зеленая инфраструктура, восстановление ландшафта, макроэкология, трофические взаимодействия в пространственном планировании.

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