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Landscape-based prediction of the occurrence of the invasive muskrat (*Ondatra zibethicus*)

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In Europe, muskrat is an invasive species that can profoundly affect lake ecosystems. We developed a landscape-based prediction model for the occurrence of muskrat based on 237 muskrat and 236 randomly selected lakes within the distribution range of muskrat in northern Sweden. We analyzed the importance of slope and cover of vegetation types for the occurrence of the muskrat at 12 spatial scales (50–1000 m) from the lakeshores. Logistic regression models that incorporated slope and percentage cover of swamps, meadows and lakeshore meadows successfully predicted the occurrence of muskrat. The importance of the predictor variables changed with increased distance from the shoreline. Our results were confirmed with an independent data set (n = 29) from the southern distribution range of the muskrat in Sweden. The prediction model can be used to assess the risk of muskrat occurrence in lakes as well as for the development of muskrat-related conservation measures.

Introduction

In Europe, the muskrat (*Ondatra zibethicus*) is an introduced North American species, which at high population densities can have profound effects on limnic ecosystems. The species was introduced into central Europe in 1905 as a game species, but through natural dispersal and further introductions it established rapidly in many other countries (Ulbrich 1930, Hoffmann 1958). Soon, damages to poorly constructed water dams and banks of roads and railroads were noted. Consequently, eradication programs for muskrats were initiated in many countries where some still continue today. In northern Europe the muskrat was introduced into Finland in 1919 (Artimo 1960) and passed the border river between Finland and Sweden a few years before 1950. Thereafter, the muskrat invaded Sweden at a rate of about 10 km per year (Danell 1977a) and continues southwards. Considering the native range of the muskrat (Erb & Perry 2003) and its reported occurrences in Europe and Eurasia (Danell 1996), the present world-wide distribution of the muskrat outside its native range is larger than the native one.

The muskrat, the brown rat *Rattus rattus* and the sika deer *Cervus nippon* have the highest potential and actual environmental and economic impact of all alien mammals in Europe, with the American mink (*Neovison vison*) having the second highest actual environmental impact (Nentwig *et al*. 2010). The American mink is also an important predator of muskrats (Brzeziński *et al*. 2010). To date no damage to infrastructure in water has been noted in northern Sweden, mainly because the road banks and dams for hydropower are of solid construction. More obvious is the reduction by muskrats of vegetation in shallow, stagnant waters where macrophytes are used as food and for construction of houses (Danell 1977b, 1978a, 1979, Smirnov & Tretyakov 1998, Connors *et al*. 2000). The muskrat is a rather strict herbivore, but in some situations, e.g. during winter when plant food is scarce, it can feed on freshwater mussels (Brander 1949, Neves & Odom 1989, Henrikson & von Proschwitz 2006, Owen *et al*. 2010). At high population densities, the muskrat has a profound impact on plant community structure in lakes (Danell 1977b), and potentially it can negatively affect rare plant species as well as endangered invertebrates, e.g. freshwater mussels. The muskrat is also one of the vectors for tularemia and other zoonoses (Sjöstedt 2007). On the other hand, the reduction of emergent vegetation, especially in waters covered by dense vegetation, may be regarded as beneficial by people living around waterbodies and using the water, while also positively affecting waterfowl (Kiviat 1978). Consequently, the abundance of muskrats is of great interest for conservation, medical risk assessment and for wetland management in general (Skyrienė & Paulauskas 2012). Firstly, knowledge of the muskrat habitat use and landscape preferences is crucial. For a limited area in coastal northern Sweden, Danell (1978b) studied habitat preferences of muskrats. A more general model on habitat selection is needed as the range of the muskrat in non-native regions is expanding. Furthermore, new analytical techniques at the landscape and regional scale facilitate such an approach.

The aim of our study is threefold. First, we tested if muskrat and random lakes can be distinguished based on topography and vegetation type along the shorelines of lakes. We hypothesized that percentage cover of vegetation types (e.g. meadows) that indicate species-rich and highly productive emergent vegetation in the shallow waters around muskrat lakes is high. Muskrat lakes should also have flatter shorelines since flat topography increases the incident of rich communities of aquatic helophytes for food and house-construction. In addition, the surroundings of muskrat lakes should have low percentage cover of coniferous forest and mires, since the presence of these indicates sparse emergent vegetation in the shallow waters. Second, we analyzed the scale dependency of muskrat responses to topography and vegetation types. We hypothesized that such responses are evident also at large scales (up to 1 km) from lakeshores, since muskrat houses frequently are located 100 m or more from the lake shore and in lakeshore meadows rich in aquatic helophytes. Finally, we developed a prediction model for muskrat occurrence based on topography and vegetation types that can be used for future muskrat management.

Methods

Study area

Our study included two regions in northern Sweden (Fig. 1). The main study area was located in the county of Norrbotten. It included all muskrat and randomly selected lakes used for the identification of landscape properties associated with the occurrence of muskrat (*see* below and Fig. 1). The second region was the municipality of Örnsköldsvik, located at the southern distribution range of the muskrat in Sweden (Fig. 1a). Both regions are predominately located in the middle boreal sub-zone, but some western localities in Norrbotten belong to the northern boreal sub-zone, and some eastern localities in the municipality of Örnsköldsvik belong to the southern boreal sub-zone (Sjörs 1999). As compared with the Örnsköldsvik region, the Norrbotten region has generally flatter topography.

Data on muskrat occurrence

Since their invasion into Norrbotten in the late 1940s, muskrats have continued to expand their

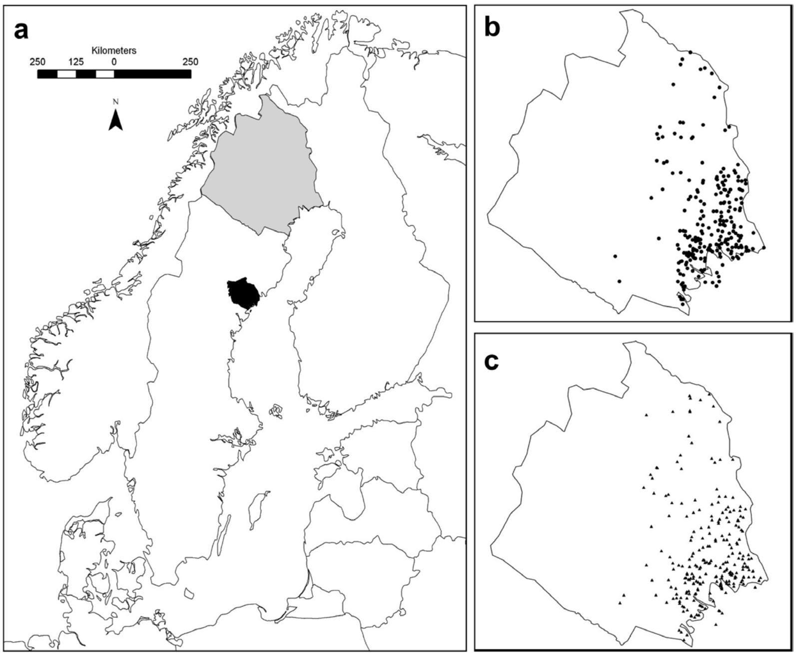

Fig. 1. Location of the study area (**a**) in the county of Norrbotten (shaded), northern Sweden, and of the 237 studied muskrat (**b**, circles) and 236 randomly selected (**c**, triangles) lakes. The municipality of Örnsköldsvik (black) is also shown in **a**. Muskrat data from Örnsköldsvik were used to validate the landscape-based muskrat model.

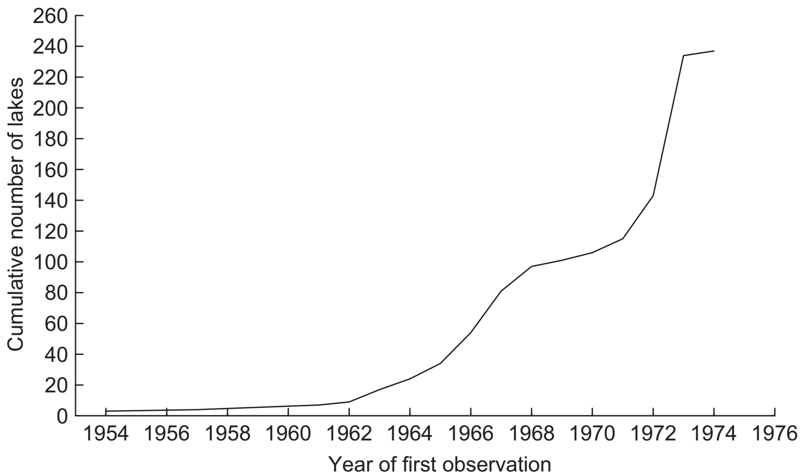

Fig. 2. Cumulated number of studied lakes with muskrat observations in 1954–1974 in the county of Norrbotten. Note that sampling effort varied among years.

range in the county (Fig. 2). Major increases in the number of colonized lakes occurred in 1965–1967 and 1971–1973 (Fig. 2). In our study, we used two different muskrat data sets. For model development, we used the data from 237 muskrat lakes (1954–1976) in the county of Norrbotten, compiled and, to a large extent, sampled by K. Danell. For the identification of potential muskrat lakes, 5 × 5 km subareas according to the Swedish National Grid were studied. Within each subarea to be checked in the field, lakes of different sizes were selected at random. Of these, lakes which were accessible within 500 m from roads or logging roads were inventoried. A lake was identified as a muskrat lake if (a) muskrat was observed, (b) burrows and/or houses were present, (c) feeding remains were found and/or (d) droppings were found (Danell 1977a). Muskrat lakes have a mean (± SD) size of 159 ± 275 ha with a mean (± SD) nearest Euclidian distance to neighboring muskrat lakes of 4.0 ± 5.2 km, and they were compared with 236 randomly selected lakes (mean size 104 ± 195 ha, nearest Euclidian distance to neighboring random lake 4.8 ± 5.1 km) that are located within the same region as the muskrat lakes (Fig. 1). In most of the muskrat lakes, a muskrat was observed only once (n = 163) or twice (n = 44), and in three lakes, muskrats have been observed for at least 10 years. We did not consider any potential extinction and re-colonization of the lakes once the were recorded as muskrat lakes. The muskrat data from Norrbotten also included ca. 20 streams with muskrat occurrence. Due to low accuracy of the coordinates of muskrat occurrence in streams, we focused our landscape analyses on lake observations. To verify our model with muskrat data from outside the county of Norrbotten, we used the data from 29 muskrat lakes (mean size 108 ± 158 ha, Euclidian distance to neighboring muskrat lake 3.2 ± 53.5 km) compiled by the municipality of Örnsköldsvik. The muskrat data from Örnsköldsvik were based on a public web-based reporting system in 2004–2005.

According to the Swedish Species Gateway (as of 4 April 2011), none of the muskrat lakes in Norrbotten has documented occurrence of red-listed freshwater mussels. However, the red-listed freshwater pearl mussel *Margaritifera margaritifera* occurred in three of the ca. 20 muskrat streams in Norrbotten.

Landscape data and analyses

In our analyses, we used three data sets on landscape information. The first landscape data used were the national elevation data for Sweden that have a ground resolution of 50 m and a vertical resolution of 1 m. Two types of vegetation maps are available for the county of Norrbotten. The Swedish Corine data (*marktäckedata*) have a ground resolution of 25 m and are based on a 2000 Landsat satellite scene with 61 land cover types including ca. 30 different vegetation types. The Corine data include no separate vegetation class for floating aquatic vegetation and emergent aquatic vegetation. Since we hypothesized that floating and emergent vegetation positively affect the occurrence of muskrats, we instead used the Vegetation Map of Norrbotten (Lantmäteriet i Norrbotten 1981) for the model development. The Vegetation Map is based on infrared aerial photographs that are verified by field control and has a minimum mapped area of 0.06 ha and distinguishes 44 vegetation and land-cover types. Since no vegetation map was available for the municipality of Örnsköldsvik, verification of our analyses based on the muskrat data from this region was performed using the Corine data only, which implied that the importance of floating and emergent vegetation for muskrat occurrence could not be tested in this region.

The habitat of muskrats includes not only lakes, but also the vegetated shorelines where they for example build their houses (Danell 1977b, Hjältén 1991). We, therefore, analyzed the importance of topography (slope) and percentage area of the vegetation types in buffer strips ranging from 50–1000 m (50, 100, 150, 200, 250, 300, 350, 400, 450, 500, 750 and 1000 m) from the shoreline. All spatial analyses were performed with the ArcGIS software (ESRI 2009). According to our hypotheses, we included the following vegetation types in the analyses: coniferous forests of the mesic dwarf shrub type (Arnborg 1990), which is the most common forest type in northern Sweden (code 13 and 56 in the Vegetation and Corine map, respectively), mires that have a low cover of herbs (code 52 and 72 in the Vegetation and Corine map, respectively), swamps (i.e. wetland areas rich in herbs) (code 54 and 70 in the Vegetation and Corine map, respectively), meadows rich in non-aquatic helophytes (code 91 and 32 in the Vegetation and Corine map, respectively) and meadows rich in aquatic helophytes (code 71 and 82 in Vegetation and Corine map, respectively).

Statistical analyses

Muskrats were observed in all analyzed muskrat lakes. In contrast, the absence of muskrats from the assigned random lakes was not confirmed. We are aware that such a bias might result in the underestimation of habitat preferences and in type II errors (Zar 1996). All muskrat data were analyzed at the level of presence/absence since no abundance data were available.

Differences in topography and vegetation type between muskrat and random lakes at all spatial scales were analyzed with the Mann-

Whitney *U*-test (Zar 1996). We used best subset logistic regression modeling to predict the occurrence of muskrats. These analyses were performed and exemplified for the 100-m buffer zone, one of the buffers that showed significant differences in all tested landscape variables (*see* results). To identify the best model, we used Akaike's information criterion (AIC) (Burnham & Anderson 2002). In the first model (Model-1), we included all predictor variables with a variance > 2. The second model (Model-2) included only the significant predictor variables from Model-1. In the third model (Model-3), we also tested the importance of potential interaction of the predictor variables. In the fourth model (Model-4), we used a random subset of the muskrat data set to build a logistic regression model and the remaining data set to validate the model. Model-4 included the same predictor variables as the best model (Model-1, Model-2 or Model-3) identified by AIC. In addition and for comparison, we developed Bayesian prediction models using Naïve Bayes Classifier (StatSoft 2011) for the occurrence of muskrat. We divided the muskrat data into building (75% of the data) and validation data sets (25% of the data). The default prior probability (naïve occupancy) for muskrat occurrence calculated from the data was 51.1%. All statistical analyses were performed using the STATISTICA software (StatSoft 2011).

Results

According to the vegetation map for the county of Norrbotten, seven of the studied lakes were rich in macrophyte vegetation including floating-leaved vegetation such as water lilies *Nuphar lutea* and *Nymphaea alba* subsp. *candida* and helophytes, e.g. common reed *Phragmites australis*, water horsetail *Equisetum fluviatile* and common club-rush *Schoenoplectus lacustris*. All of these lakes were muskrat lakes. As predicted, muskrat lakes compared with random lakes were characterized by flatter lake shores as well as by a higher percentage area of swamps rich in herbs and of meadows rich in aquatic and non-aquatic helophytes in the surrounding area (Figs. 3 and 4). In addition, as compared with random lakes in the surrounding area, muskrat lakes had a lower percentage of mires and of coniferous forest of the mesic dwarf shrub type (Figs. 3 and 4). The significance of these differences between muskrat and random lakes was scale dependent. Slope of lake shores was non-significant at a distance > 500 m from the shore line (Fig. 4). The importance of the percentage area of swamps rich in herbs and coniferous forest of the mesic dwarf shrub type decreased with increased distance, but was significant at all scales (Fig. 4). In contrast, the importance of mires (negatively affecting muskrat presence) and of the two meadow types (positively affecting muskrat presence) increased with increased distance from the shoreline (Fig. 4). There are no trends in our data that the vegetation preferences of muskrat might have changed over time (data not shown).

Topography and vegetation types successfully predicted muskrat occurrence in Norrbotten (Table 1). The best model (lowest AIC and lowest number of explanatory variables) was Model-2 which included four of the six predictor variables, i.e. slope, percentage cover of swamps, meadows and lakeshore meadows. Of models Model-1–Model-3, Model-2 had also a slightly higher percentage of correct classifications and a higher value of Cohen's $\varkappa$ than the other models. The model based on the validation data set used four predictor variables and resulted in 65.8% correct classifications (Table 1) which was only 3.5% less as compared with the model based on the building data set. The results of the logistic regression model were confirmed by the Bayesian model. Here, the model with all predictor variables resulted in 68.3% correct classifications (Cohen's $\varkappa$ = 0.36). The Bayesian model with the four predictor variables included in the best logistic regression (Model-2) resulted in 62.6% correct classifications (Cohen's $\varkappa$ = 0.23). Using equal prior probabilities for muskrat occurrence and absence resulted in the same results.

Vegetation properties of the muskrat lakes in Norrbotten and in Örnsköldsvik were similar at the 50-m scale (Table 2). The lakeshores in Örnsköldsvik were steeper than those in Norrbotten, both at the 50- and 1000-m scales (Table 2). At the largest scale (1000 m), vegetation properties of the muskrat lakes differed between the two regions (Table 2).

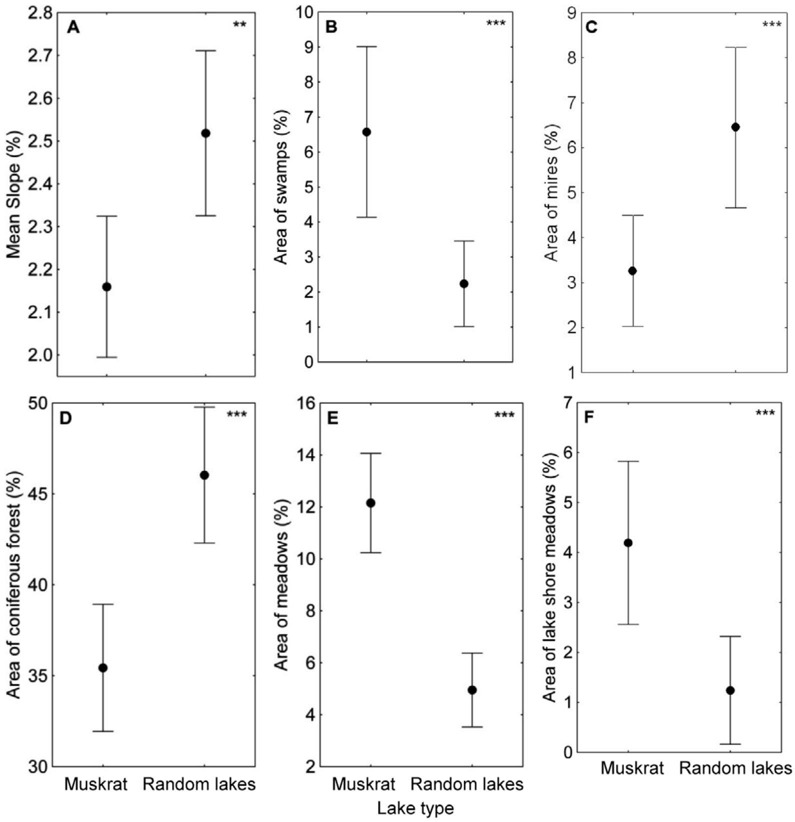

Fig. 3. Topographic and vegetation properties (mean ± 2 SE) of muskrat (n = 237) and random lakes (n = 236) in the county of Norrbotten within a 50-m buffer strip along the shoreline. Significant differences between muskrat and random lakes based on the Mann-Whitney *U*-test are indicated with asterisks (** $p < 0.01$ and *** $p < 0.001$).

Table 1. Best subset logistic regression models for the occurrence of muskrat (*Ondatra zibethicus*) based on topography and vegetation type within a 100-m buffer zone from the shoreline of the studied lakes. A dash indicates that the respective variable was not included in the model. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For Model-4 a random subset of the data set was used to build the model and the remaining data set was used to validate the model.

	Model				
	1 (n = 473)	2 (n = 473)	3 (n = 473)	4 (model building) (n = 246)	4 (validation) (n = 227)
χ^2	79.4***	76.7***	77.8***	47.8***	
df	6	4	5	4	
AIC	602.8	601.5	602.3	310.1	
Classifications (% correct)	68.0	68.5	67.8	69.3	65.8
Cohen's $\varkappa$	0.36	0.37	0.36	0.38	0.32
Estimate					
Intercept	0.006	–0.189	–0.176	–0.366	
Slope	–0.172*	–0.169*	–0.168*	–0.152	
Coniferous forest	–0.002	–	–	–	
Swamps	0.029*	0.032**	0.032**	0.051**	
Mires	–0.018	–	–	–	
Meadows	0.051***	0.055***	0.052***	0.056***	
Lakeshore meadows	0.031	0.034*	0.018	0.044	
Lakeshore meadows × meadows	–	–	0.002	–	

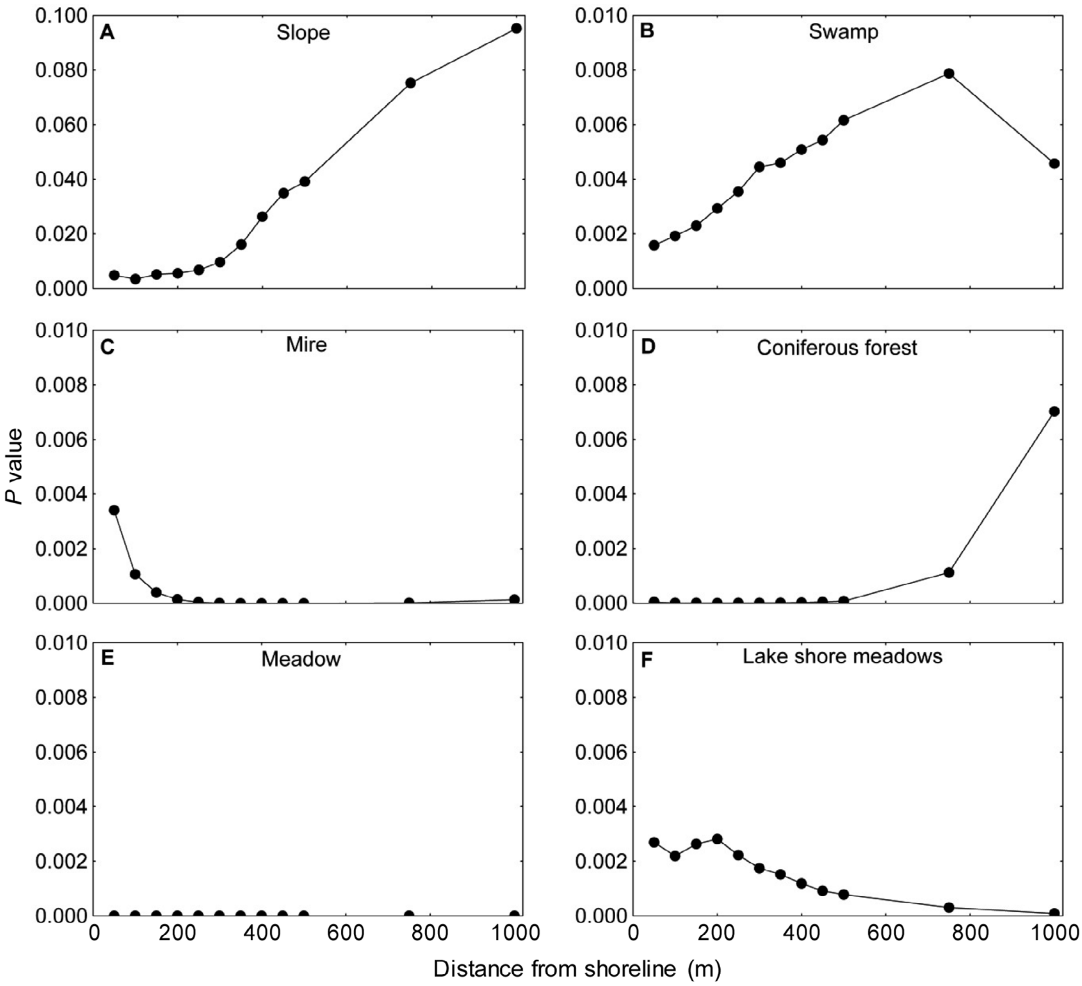

Fig. 4. The significance of landscape properties at 12 distances (50–1000 m) from the shoreline for the occurrence of muskrat in the studied lakes in the county of Norrbotten. The *p* values (Mann-Whiteny *U*-test) indicate the significance level of the differences in landscape properties between the muskrat and random lakes (*see* Fig. 3).

Table 2. Topographic and vegetation properties of the Norrbotten muskrat lakes and the verification muskrat lakes from the municipality of Örnsköldsvik at two spatial scales (50 and 1000 m). Differences between the two regions were tested using the Mann-Whitney *U*-test (* $p < 0.05$, *** $p < 0.001$). Coniferous forest of the mesic dwarf shrub type was not present within the studied buffers in the Örnsköldsvik region.

Variable (%)	Scale 50 m				Scale 1000 m			
	Norrbotten		Örnsköldsvik		Norrbotten		Örnsköldsvik	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Slope	2.16***	0.08	3.59	0.29	2.61***	0.08	5.10	0.30
Coniferous forest	35.43	1.75	–	–	48.48	1.07	–	–
Swamps	6.58	1.22	4.30	1.96	0.80***	0.16	1.25	0.45
Mires	3.26	0.62	0.83	0.62	3.36***	0.23	0.07	0.05
Meadows	12.15	0.96	11.05	2.81	8.87*	0.67	3.20	0.41
Lakeshore meadows	4.19	0.82	–	–	0.74	0.14	–	–

Discussion

Species traits and life-history strategies of invasive species are identified with increased success (Kolar & Lodge 2001). In contrast, our knowledge on the susceptibility of ecosystems to invasive species is still limited. The discussion on this topic focuses mainly on whether species-rich or species-poor ecosystems are more susceptible to invasion (Levine 2000, Byers & Noonburg 2003). Increasing our understanding of the landscape ecology and habitat preferences of invasive species is fundamental for their successful management (With 2002, Andersen *et al*. 2004). So far, there is no prediction model for any of the environmentally and economically most important invasive species in Europe, i.e. muskrat, brown rat, sika deer and American mink (Nentwig *et al*. 2010) outside their native distribution range. In this study, we developed such a prediction model for the muskrat. The known preferences of muskrats for local habitats rich in aquatic emergent vegetation (e.g. *E. fluviatile* and *S. lacustris*) (Danell 1977b, 1978a, Smirnov & Tretyakov 1998) were also evident at the landscape scale in our study. Muskrat and random lakes differed significantly in vegetation properties along the shoreline. The muskrat occurrence could successfully be predicted by vegetation properties and topography of the lake shores. According to our model, lakes with extensive areas of meadows rich in herbs and lakeshore meadows rich in helophyte vegetation (e.g. *E. fluviatile* and *S. lacustris*) are especially suitable for muskrats. Lakeshore topography is an important additional explanatory variable. The flatter the shoreline, the higher the probability for lakeshore meadows occurring at large distance (> 500 m) from the shoreline. The vegetation properties of lakeshores in Norrbotten and Örnsköldsvik differed at the large spatial scale (1000 m). The topography is different in these two regions, with Örnsköldsvik having more hilly areas than Norrbotten. Hence, it is not surprising that the topography and vegetation properties of the muskrat lakes differed between the regions at the 1000-m scale. The reliability of our model is supported by the similarity between both regions regarding topography and vegetation properties of the muskrat lakes at the 50-m scale.

Muskrat research in Sweden and other Nordic countries has been almost negligible since the mid-1980s and our knowledge of current muskrat lakes is limited. Furthermore, during the last two decades populations have been low for unknown reasons (K. Danell pers. obs.), but limitation by e.g. food, parasites and predation cannot be excluded (Skyrienė & Paulauskas 2012). Therefore, the old data set used here was the best available and it represents muskrat habitat selection during expansion phases. In our analyses, it is possible that muskrats actually occurred or are still occurring at low numbers in the selected random lakes. This underestimation of muskrat occurrence would lower the accuracy of our predictions. A future study should hence be preferably based on data from occurrences and true absences. Prediction models for the occurrence of the semi-aquatic muskrat could further be improved by incorporating information on the connectivity of lakes, either in terms of connecting streams or preferred habitats. Hence, as compared with random lakes, muskrat lakes should be characterized by higher connectivity to other lakes with preferred habitat properties. At the local scale, lake water properties, e.g. related to the trophic status of muskrat lakes, could also act as predictor variables to refine the prediction models presented here.

Muskrat is a potential predator of freshwater mussels including the freshwater pearl mussel *M. margaritifera* (Brander 1949, Neves & Odom 1989, Henrikson & von Proschwitz 2006, Owen *et al*. 2010). Red-listed freshwater mussels in the county of Norrbotten occur mainly in streams. Confirmed coexistence of muskrats and *M. margaritifera* in three streams indicate the risk that spreading muskrats might prey upon freshwater mussels. Muskrats are persistently spreading southwards in Sweden at a rate of ca. 10 km per year (Danell 1996). In 2011, muskrats were observed in the northern part of the county of Gävleborg (Swedish Species Gateway), which is ca. 200 km south of the municipality of Örnsköldsvik. In addition, it is likely that muskrats could also enter Sweden from the south via Denmark or from the east via the Åland Islands that are located between Sweden and Finland. If they disperse southwards or enter Sweden from the south or the east, they might potentially prey upon on lake-living freshwater mussels like the red-listed depressed river mussel *Pseudanodonta complanata* Rossmaessler, which does not occur in the county of Norrbotten. Whether the muskrat indeed is a threat to freshwater mussels in Sweden needs to be investigated. Our knowledge of the nature conservation value of specific lakes (e.g. related to the occurrence of red-listed freshwater mussels or macrophytes) is continually growing. Considering the potential profound effects of muskrats on aquatic systems, especially during the initial years of invasion (Danell 1996), and their role as vectors for zoonoses (Sjöstedt 2007), it is important to have a ready management tool in case muskrats spread further and/or the population densities increase. As a first step and as a precaution, it is important to assess the risk of a specific lake with high conservation values to be invaded by the muskrat. This can be accomplished by assessing the area and proportion of vegetation stands preferred by muskrats from aerial photographs or even high-resolution satellite images. In addition, vegetation maps that include detailed information on aquatic and shoreline vegetation are increasingly available in Sweden and other Nordic countries. Incorporating such information in the prediction model presented here can be used to assess the risk of muskrat occurrence in specific lakes and to decide on the potential management of muskrat in such lakes.

Our study showed that the occurrence of invasive species can be successfully predicted. It should be tested if the occurrence of other important invasive species such as the sika deer, the semi-aquatic nutria *Myocastor coypus* and the American mink can also be predicted with a landscape approach as used in our study.

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References

Andersen, M. C., Adams, H., Hope, B. & Powell, M. 2004: Risk analysis for invasive species: general framework and research needs. — *Risk Analysis* 24: 893–900.

Arnborg, T. 1990: Forest types of northern Sweden. Introduction to and translation of “Det nordsvenska skogstypsschemat”. — *Vegetatio* 90: 1–13.

Artimo, A. 1960: The dispersal and acclimatization of the muskrat, *Ondatra zibethicus* (L.), in Finland. — *Papers on Game Research* 21: 1–101.

Brander, T. 1949: Om bisamråttan i Finland ur naturskyddssynpunkt. — *Finlands Natur* 8: 12–23.

Brzeziński, M., Romanowski, J., Żmihorski, M. & Karpowicz, K. 2010: Muskrat (*Ondatra zibethicus*) decline after the expansion of American mink (*Neovison vison*) in Poland. — *European Journal of Wildlife Research* 56: 341–348.

Burnham, K. & Anderson, D. R. 2002: *Model selection and inference. A practical information-theoretic approach*. — Springer, New York.

Byers, J. E. & Noonburg, E. G. 2003: Scale dependent effects of biotic resistance to biological invasion. — *Ecology* 84: 1428–1433.

Connors, L. M., Kiviat, E., Groffman, P. M. & Ostfeld, R. S. 2000: Muskrat (*Ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. — *American Midland Naturalist* 143: 53–63.

Danell, K. 1977a: Dispersal and distribution of the muskrat *Ondatra zibethicus* in Sweden. — *Viltrevy* (*Stockholm*) 10: 4–26.

Danell, K. 1977b: Short-term plant successions following colonization of a northern Swedish lake by muskrat *Ondatra zibethica*. — *Journal of Applied Ecology* 14: 933–948.

Danell, K. 1978a: *Ecology of the muskrat in Northern Sweden*. — Ph.D. thesis, University of Umeå.

Danell, K. 1978b: Food habitat of the muskrat *Ondatra zibethicus* in a Swedish lake. — *Annales Zoologici Fennici* 15: 177–181.

Danell, K. 1979: Reduction of aquatic vegetation following the colonization of a northern Swedish lake by muskrat *Ondatra zibethicus*. — *Oecologia (Berlin)* 38: 101–106.

Danell, K. 1996: Introductions of aquatic rodents: Lessons of the muskrat *Ondatra zibethicus* invasion. — *Wildlife Biology* 2: 213–220.

ESRI 2009: *ArcGIS 9.3.1. ArcInfo*. — Environmental Systems Research Institute Inc., Redlands, CA, USA.

Erb, J. & Perry, H. R. Jr. 2003: *Muskrats*. — In: Feldhamer, G. A., Thompson, B. C. & Chapman, J. A. (eds), *Wild mammals of North America: biology, management, and conservation*: 311–348. The Johns Hopkins University Press.

Henrikson, L. & von Proschwitz, T. 2006: Bisam — en växtätare med smak för musslor. — *Fauna och Flora* 101: 2–7.

Hjältén, J. 1991: Muskrat (*Ondatra zibethica*) territoriality, and the impact of territorial choice on reproduction and predation risk. — *Annales Zoologici Fennici* 28: 15–21.

Hoffmann, M. 1958: *Die Bisamratte: ihre Lebensgewohnheiten, Verbreitung, Bekämpfung und wirtschaftliche Bedeutung*. — Akademische Verlagsgesellschaft Geest & Portig, Leipzig.

Kiviat, E. 1978: Vertebrate use of muskrat lodges and burrows. — *Estuaries and Coasts* 1: 196–200.

Kolar, C. S. & Lodge, D. M. 2001: Progress in invasion biology: predicting invaders. — *Trends in Ecology and Evolution* 16: 199–204.

Lantmäteriet i Norrbotten 1981: *Försök med Vegetationskartering i Norrbottens län*. — Planeringsavdelningens rapportserie 1981:13, Luleå.

Levine, J. M. 2000: Species diversity and biological invasions: relating local process to community pattern. — *Science* 288: 852–854.

Nentwig, W., Kühnel, E. & Bacher, S. 2010: A generic impact-scoring system applied to alien mammals in Europe. — *Conservation Biology* 24: 302–311.

Neves, R. J. & Odom, M. C. 1989: Muskrat predation on endangered freshwater mussels in Virginia. — *The Journal of Wildlife Management* 53: 934–941.

Owen, C. T., McGregor, M. A., Cobbs, G. A. & Alexander, J. E. Jr. 2010: Muskrat predation on a diverse unionid mussel community: impacts of prey species composition, size and shape. — *Freshwater Biology* 56: 554–564.

Sjörs, H. 1999: The background: geology, climate and zonation. — In: Rydin, H., Snoeijs, P. & Diekmann, M. (eds.), *Swedish plant geography*: 5–14. Svenska Växtgeografiska Sällskapet, Uppsala.

Sjöstedt, A. 2007: Tularemia: history, epidemiology, pathogen physiology, and clinical manifestations. — *Annals of the New York Academy of Sciences* 1105: 1–29.

Skyrienė, G. & Paulauskas, A. 2012: Distribution of invasive muskrats (*Ondatra zibethicus*) and impact on ecosystem. — *Ekologija* 58: 357–367.

Smirnov, V. V. & Tretyakov, K. 1998: Changes in aquatic plant communities on the island of Valaam due to invasion by the muskrat *Ondatra zibethicus* L. (Rodentia, Mammalia). — *Biodiversity and Conservation* 7: 673–690.

StatSoft 2011: STATISTICA (data analysis software system). — Statsoft Incorporation, Tulsa.

Ulbrich, J. 1930: *Die Bisamratte, Lebenweise, gang ihrer Ausbreitung in Europa, wirtschaftliche Bedeutung und Bekämpfung*. — C. Heinrich, Dresden.

With, K. A. 2002: The landscape ecology of invasive spread. — *Conservation Biology* 16: 1192–1203.

Zar, J. H. 1996: *Biostatistical analysis*. — Prentice-Hall, Inc., London.