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REVIEW

North American Beaver (*Castor canadensis* Kuhl) key habitat characteristics: review of the relative effects of geomorphology, food availability and anthropogenic infrastructure

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ABSTRACT
The North American beaver is considered a keystone species because its behaviour leads to profound changes in the wetland systems within forested landscapes. Such changes influence species composition and their interactions. However, in some cases, beavers are considered as an important source of disturbance and conflict with anthropogenic activities. In this paper, we reviewed regional studies using geomorphology, food availability and anthropogenic infrastructure on spatial modelling of beaver habitat. Even though all studies used different sets of variables and methodologies, important factors affecting beaver occurrence or abundance are mainly stream gradient, watershed size and hardwood cover that is adjacent to the streams. However, the identification of key habitat indicators often varies between studies depending upon the object being modelled (colonies vs. dams), the geomorphological characteristics of the region, and the scale of the study area. Recent developments in geomatics and improved data quality now allow spatial modelling of beaver habitat across larger areas, and make models using at least stream gradient and forest cover types more accessible to managers. Such large-scale predictive beaver habitat models could have valuable applications for the prevention of infrastructure damage and related costs, and for managing wildlife species that rely upon beaver ponds.

RÉSUMÉ
Le castor du Canada est considéré comme une espèce clé car son comportement cause d'importantes modifications aux milieux humides au sein des paysages forestiers. De tels changements influencent la composition des espèces ainsi que leurs interactions. Cependant, dans certains cas, les castors sont considérés comme une source importante de perturbation et de conflit avec les activités anthropiques. Dans cet article, nous faisons la recension des études régionales qui ont utilisé la géomorphologie, la disponibilité de ressources alimentaires et la présence d'infrastructures anthropiques pour réaliser une modélisation spatiale de l'habitat du castor. Même si les études ont utilisé des variables et des méthodologies différentes, les principaux facteurs affectant l'occurrence ou l'abondance du castor sont le gradient des ruisseaux, la superficie du bassin hydrographique et le couvert de peuplements feuillus adjacents aux cours d'eau. Cependant, l'identification des principaux indicateurs d'habitat varie selon les études en fonction de la variable modélisée (huttes ou barrages), des caractéristiques géomorphologiques de la région et de la taille de la zone d'étude. Les développements récents de la géomatique et l'amélioration de la qualité des données disponibles permettent maintenant la modélisation spatiale de l'habitat du castor pour de grandes régions et rendent les modèles utilisant au moins le gradient des ruisseaux et les types de couverts forestiers plus accessibles aux gestionnaires. De tels modèles prédictifs de l'habitat du castor à grande échelle pourraient avoir des applications importantes pour la prévention des dommages aux infrastructures et des coûts qu'ils engendrent, ainsi que pour la gestion des espèces fauniques qui dépendent de la présence d'étangs de castors.

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Introduction

The North American beaver (*Castor canadensis* Kuhl) is one of two extant beaver species (the European beaver is *C. fiber* L.). Historically valued for its fur, *C. canadensis* is generally considered a keystone species of forest, aquatic and riparian ecosystems across its native North American range. The beaver's ability to modify its environment by constructing dams on streams enables the species to occupy a variety of natural and anthropogenic habitats (Baker and Hill 2003). Beaver

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dams modify and create wetlands while significantly changing the structure and dynamism of the riparian environment by increasing exchanges between surface and groundwater sources (Fortin et al. 2001; Burchsted et al. 2010; Majerova et al. 2015). The resulting mosaic of cyclically occupied and abandoned beaver ponds provides shelter, food and breeding habitat to many invertebrates (McDowell and Naiman 1986), fishes (Snodgrass and Meffe 1998), amphibians (Stevens et al. 2007), birds (Aznar and Desrochers 2008; Nummi and Hahtola 2008; Soto et al. 2012; Nummi and Holopainen 2014), mammals (Nummi et al. 2011) and waterfowl (McCall et al. 1996). Beaver activity therefore constitutes a natural disturbance regime, which enhances landscape heterogeneity and diversity (Cunningham et al. 2006; Burchsted et al. 2010; Westbrook et al. 2011).

Despite the importance of its ecological role, the beaver is often perceived as a 'nuisance' species (Curtis and Jensen 2004; Malison et al. 2014, 2016; Westbrook et al. 2017). Beavers frequently make use of logging roads and culverts as foundations for their dams, subsequently causing flooding and damage to trails, roads and commercially valuable forests (Fortin et al. 2001). In the early 1980s, damage that was related to beaver activity in the United States was estimated to exceed 75 million US dollars per year (about 88 million $CAN) (Miller 1983, cited in Novak 1987). The recent cost of repairing infrastructure that had been damaged by beavers remains high due to the continuing growth of beaver populations (Fortin and Lizotte 2007).

After centuries of exploitation, reduction and local extinctions of beaver populations, improved management and conservation practices have allowed this species to regain its previous importance within North American forests (Novak 1987). For instance, an aerial inventory of beaver colonies that was conducted from 1989 to 1994 in Quebec (Canada) estimated the total beaver population to be over 700,000 individuals (Lafond and Pilon 2004). In the Abitibi-Témiscamingue region of western Quebec, within a two-year period (1987–1989) during which trapping pressure was significantly decreasing because of falling fur prices, beaver colony density increased from 5.4 to 7.4 colonies/10 km^2 (Lafond et al. 2003).

Beavers have been the subject of scientific observation and research for many years, leading to the advancement of beaver ecology and the understanding of their functions in the forested regions of North America, as well as the development of models for classifying and assessing the quality of their habitat. However, a lack of consensus remains in the scientific literature regarding the identification and importance of habitat variables at both the scale of the forest stand and the landscape. According to Curtis and Jensen (2004), this disparity can be explained by differences in the extent of study areas and the vegetation classification measurements that were made across studies. This confounding information increases the level of difficulty for managers seeking to mitigate the negative effects of beaver on forest roads, because they are unable to easily identify the areas or structures that are most at risk of beaver colonization.

The main objective of this literature review was to identify the dominant habitat determinants most frequently mentioned in studies that are related to beaver habitat selection, taking into account varying methodological or geographical considerations in the different studies. More specifically, we aimed to present a review of factors affecting beaver habitat use, according to three broad categories: 1) geomorphological variables; 2) factors related to food availability; and 3) variables concerning anthropogenic infrastructure.

Methodology

To conduct an inventory of studies on beaver habitat, we searched online databases (ISI Web of Science, ScienceDirect and JSTOR) as a means of ensuring the inclusion of all archived and recent publications (in English or French) that specifically identify beaver habitat variables. The search was performed using keywords 'beaver' AND 'habitat' OR 'model.' To generate the most exhaustive list possible, we also collected relevant theses and reports that were cited in the aforementioned scientific articles.

From over 1500 articles dealing with the beaver and its habitat in North America, we selected only the studies that presented beaver habitat classifications, habitat selection or habitat use models, or which identified the most significant habitat factors for this species. The habitat factors that were described are based upon results obtained from the 12 modelling studies that met the selection criteria. Habitat quality indices that were published solely on the basis of literature reviews, or which arose from mathematical models, were excluded from this review.

Results

Of the 12 reviewed studies, half modelled the presence or abundance of dams as a response variable (Table 1). The remaining studies modelled the density of colonies or potential sites for beaver occurrence.

Table 1. Selected beaver habitat modelling studies.

Study Code	Authors	Study Area	Hydrographic System	Vegetation Type/Ecoregion	Colony Density (per km)	Response Variable
1	Suzuki and McComb (1998)	Drift Creek Basin, Oregon (Lincoln County)	179 km^2 watershed, (stream length of 65 km)	Marine West Coast Forests	2.6	Number of dams potential sites per section
2	Slough and Sadleir (1977)	Northern British Columbia	45 stream sections (145 km)	Northwestern Forested Mountains		Number of potential sites per section
			136 lakes (1830 km of shoreline)	Northwestern Forested Mountains		Number of potential sites per lake
3	McComb et al. (1990)	Long Creek Basin, Oregon (East)	Watershed less than 750 ha (stream length of 98 km)	Shrub-dominated Steppes/ Northwestern Forested Mountains	0.14	Presence/Absence of dams
4	Beier and Barrett (1987)	Truckee River Basin, Nevada & California	600 km^2 watershed, (stream length of 153 km)	Mixed coniferous forest/Northwestern Forested Mountains		Presence of colonies (active, abandoned potential sites)
5	Dieter and McCabe (1989)	Big Sioux, South Dakota	45 km of the Big Sioux River (1–2% gradient)	Prairie/Great Plains		Presence/Absence of lodges
6	Barnes and Mallik (1997)	Swanson River Basin, Northern Ontario	238 km^2 watershed (stream length of 200 km)	Boreal Forest/Northern Forests		Presence of dams (active, abandoned, unoccupied sites)
7a	Cotton (1990)	North Shore of the St. Lawrence River, Quebec	Streams located in 49 trapping units	Boreal forest/Northern Forests		Density of colonies (per 4 km^2)
7b	Cotton (1990)	Papineau-Labelle Wildlife Reserve, Quebec	471 stream sections (stream length of 82 km)	Mature hardwood forest/Eastern Temperate Forests	0.82	Density of colonies (per 4 km^2)
7c	Cotton (1990)	Gatineau Park, Quebec	372.5 km of stream	Mature hardwood forest/Eastern Temperate Forests	0.98	Density of colonies (per 4 km^2)
8	Jensen et al. (2001)	Northern and Southern New York State	St-Lawrence Plain Ecozone (4 514 km^2)/Appalachian Plateau Ecozone (32 212 km^2)	Northern hardwood/Eastern Temperate Forests	Plain: 0.38–0.56/km^2 Plateau: 0.09–0.24/km^2	Presence of dams in culverts
9	Curtis and Jensen (2004)	Northern and Southern New York State	St-Lawrence Plain Ecozone (4 514 km^2)/Appalachian Plateau Ecozone (32 212 km^2)	Northern hardwood/Eastern Temperate Forests		Presence of dams within 200 m from roads
10	Howard and Larson (1985)	Prescott Peninsula, Massachusetts	60 km^2 study area, watershed less than 750 ha, (stream width less than 8 m)	Mixed forest/Eastern Temperate Forests	0.83	Density of colonies
11	Jakes et al. (2007)	Savannah River Site, High coastal plains, South Carolina	800 km^2 study area, (stream length of 291 km, < 3% gradient), 3^{rd}-order basin	High coastal plains/Eastern Temperate Forests		Presence/Absence of dams
12	Lapointe St-Pierre et al. (2017)	Québec, south of the 51st parallel	Six different ecoregions on a 306 155 km^2 study area	Boreal and temperate forests		Number of dams in 1,025 25 km2 plots

Although the geographic range of the beaver extends into at least a portion of 13 of the 15 major ecological regions (Ecoregions level I) that were designated by the Commission for Environmental Cooperation in North America (Commission for Environmental Cooperation 1997), the 12 modelling studies that have been analyzed here are concentrated in only five of these ecoregions (Figure 1). The westernmost study was conducted in Oregon by Suzuki and McComb (1998). Their research was located in the Marine West Coast Forests (Ecoregion 7), an ecoregion with very humid climate that is dominated by mountainous topography, and which is bordered by coastal plains (Commission for Environmental Cooperation 1997). Located immediately to the east of the first study, the Northwestern Forested Mountains (Ecoregion 6) contains three of the studies that were examined in this review, including those of Slough and Sadleir (1977), McComb et al. (1990) and Beier and Barrett (1987). This ecoregion consists of cold, humid mountains and plateaus that are separated by wide valleys and lowlands, with climatic conditions ranging from sub-arid to arid (Commission for Environmental Cooperation 1997).

The central part of the beaver's range has not been well documented by habitat modellers. The only study in this general area (Dieter and McCabe 1989) was located in South Dakota, which is on the western edge of the Great Plains (Ecoregion 9). The dominant vegetation type is grassland, with a sub-humid to semi-arid climate and relatively flat topography (Commission for Environmental Cooperation 1997).

In eastern North America, there are three studies (Cotton 1990; Barnes and Mallik 1997; Lapointe St-Pierre et al. 2017), which were conducted in the Northern Forests (Ecoregion 5). This region is located within the Canadian Shield and is characterized by vast boreal forest stands, hilly terrain and a high density of lakes (Commission for Environmental Cooperation 1997). Summers are warm, but winters are long and cold. Cotton (1990) modelled beaver habitat in three locations in Quebec: the first was located in Ecoregion 5, while the other two sites were found at the limit of the Eastern Temperate Forests (Ecoregion 8). The latter ecoregion contains the largest number of beaver habitat-modelling studies (Howard and Larson 1985; Cotton 1990; Jensen et al. 2001; Curtis and Jensen 2004; Jakes et al. 2007). Although specific study sites show regional habitat variations at the local scale, this ecoregion is distinguished by a generally warm, humid, temperate climate and relatively dense and diverse forests

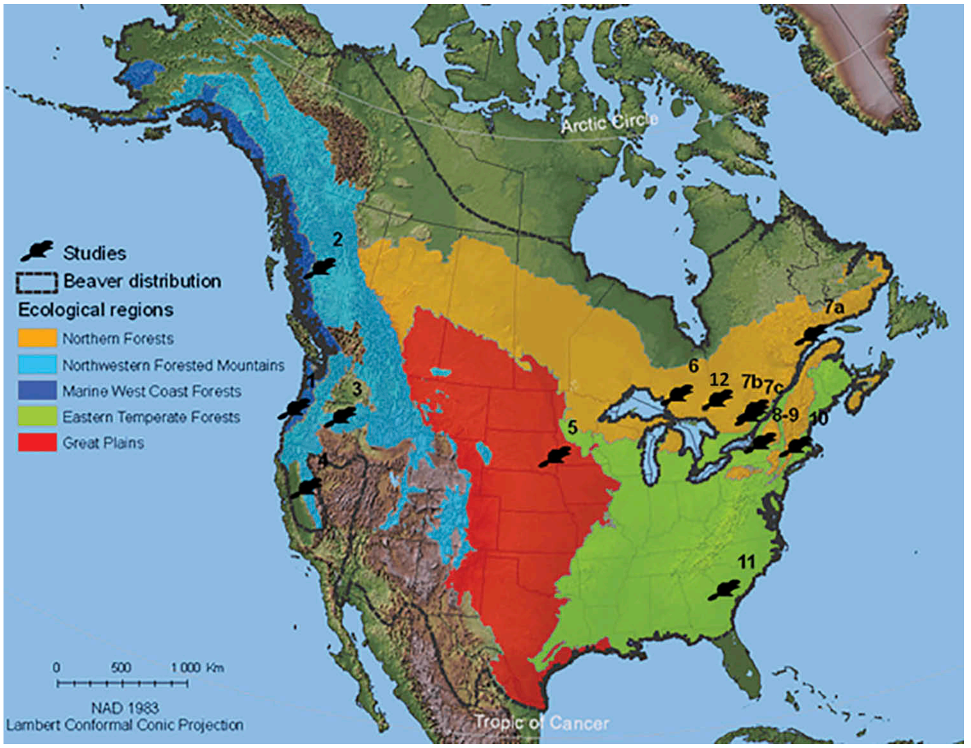

Figure 1. Geographic range of the beaver (*Castor canadensis* Khul) in North America (Patterson et al. 2007) and the locations of beaver habitat modelling studies (Table 1), according to the ecological regions of North America. (1) Suzuki and McComb (1998), (2) Slough and Sadleir (1977), (3) McComb et al. (1990), (4) Beier and Barrett (1987), (5) Dieter and McCabe (1989), (6) Barnes and Mallik (1997), (7a) Cotton (1990) Côte-Nord, (7b) Cotton (1990), Papineau-Labelle Reserve, (7c) Cotton (1990), Gatineau Park, (8) Jensen et al. (2001), (9) Curtis and Jensen (2004), (10) Howard and Larson (1985), and (11) Jakes et al. (2007), (12) Lapointe St-Pierre et al. (2017).

(Commission for Environmental Cooperation 1997). The Appalachian landscape dominates the northwest portion of the ecoregion, while the central section contains a combination of plains and rolling hills. The other eight ecoregions, where no beaver habitat modelling studies were conducted, cover about 30% of the species range. Most of this territory is in the Taiga region (Ecoregion 3), where the abundance of lakes and wetlands attracts many species of nesting birds (Commission for Environmental Cooperation 1997), which are potentially associated with beaver ponds. The southern reaches of the beaver's range, where habitat models are also missing, consists primarily of the North American Deserts (Ecoregion 10), which are characterized by marginal beaver habitat that is limited to low growing shrubs and herbaceous plants (Commission for Environmental Cooperation 1997).

General habitat characteristics

Some broad characteristics of the beaver habitat, e.g., minimum home range size, fluctuations in water supply and stream type, were surprisingly not included in the modelling studies that were considered in this literature review. Nevertheless, they have been addressed in other descriptive studies of beaver habitat and are briefly summarized here.

Home range size and foraging distance from streams

Home range size of beaver may depend upon sex, age, social organization of the family unit, type of habitat, or season (Baker and Hill 2003; McClintic et al. 2014). As an example, McClintic et al. (2014) showed that mean home range size for 23 radio-tracked beavers in Alabama was 11.86 ± 5.66 ha, but increased to 20.89 ± 26.54 ha if they considered three unusually large home ranges. Boyce (1981) observed a minimum distance of 0.48 km between beaver colonies on Alaskan rivers. In his habitat quality model, Allen (1983) assumed that a minimum of 0.8 km of stream length or 1.3 km^2 of lake area must be available for beaver colonization.

A beaver's foraging effort to obtain woody plants decreases with distance from the edge of a watercourse (Martell et al. 2006), such that its behaviour corresponds to the predictions of a central-place foraging model (Jenkins 1980; McGinley and Whitham 1985). According to dendroecological studies at Lake George, in the Parc des Grands-Jardins (Quebec), which were conducted by Bordage and Fillion (1988), the distance travelled to acquire woody vegetation is limited by topography, which determines how easily beavers can transport timber. Within their territory, beavers begin by foraging in places with the fewest barriers and where preferred species are most abundant (Bordage and Fillion 1988). The foraging distances vary widely across studies, but most agree that beaver will remain within 100 m of the shore (Allen 1983; Jenkins 1980; McGinley and Whitham 1985).

Type of watercourse

A slight variation in water level can have substantial effects upon beavers. Although the construction of dams allows beavers to control the stability and the depth of the watercourse to some degree, they are unable to colonize streams or rivers that are very deep or have extreme water-level fluctuations (Slough and Sadleir 1977). According to Allen (1983), reservoirs are also inadequate habitat for the beaver because they are generally subject to pronounced water level fluctuations.

Comparing the influence of different types of water bodies (lakes, rivers, streams, etc.) is hindered due to the range of classification systems that have been used across studies; however, these variables are commonly regarded as less important than other habitat factors (Cotton 1990). Research conducted by Traversy (1976) in James Bay (Quebec) nevertheless indicated that streams provide habitat that is superior to lakes, as a result of the higher quality and greater vegetation abundance of the former. Moreover, Traversy (1976) regarded lakes as a transitional habitat that was used temporarily by beavers before colonizing new streams. In order to be suitable for beavers, the shoreline of a large lake must consist of a diverse set of sheltered bays, which are protected from wave action (Allen 1983).

The importance of each stream within a watershed can be characterized using a hierarchical classification of all the branches of a hydrographic system. The most widely used classification system is that of Strahler (1957), which assigns an increasing rank to watercourses in a hydrological network, from streams with no tributaries (order 1) to large rivers with many feeder streams. Beavers tend to build their dams on 4th-order streams or lower, i.e., 3rd-, 2nd- and 1st-order. On higher-order rivers (i.e., 5th-order), dams are at risk of being destroyed by rising water levels and spring floods (Naiman et al. 1986). In Oregon, Bruner (1990, cited in Suzuki and McComb 1998) reported that nearly all dams that were built on 4th- and 5th-order streams were destroyed annually.

Geomorphological habitat variables

Stream gradient

The stream gradient is commonly defined as the slope between two points along a stream, divided by the distance between the points. All of the reviewed studies here have included the stream gradient in their analyses, except Dieter and McCabe (1989), who omitted this variable due to the relative consistency of the gradient along the Big Sioux River, South Dakota. Here, stream gradient values ranged from 1 to 2%. In terms of its importance for characterizing beaver habitat and the direction of the relationship (Table 2), stream gradient is the most commonly recurring variable that was encountered among the studies: habitat suitability consistently decreases with an increasing stream gradient. For example, Howard and Larson (1985) identified the stream gradient as significantly important in habitat selection, and a similar result was obtained on the same study area by Remar (2013). Beier and Barrett (1987) likewise observed that active beaver colonies in their study were located along streams with gradients that were significantly lower than those of uncolonized river segments. Suzuki and McComb (1998) did not record any dam on a stream with a gradient of more than 10%. They concluded that a gradient of 3% is optimal. Northcott (1964) also observed that no colony was located on streams where the gradient exceeded 4%. In the Papineau-Labelle Wildlife Reserve in Quebec, Cotton (1990) obtained a positive correlation between the density of beaver colonies and the density of streams with gradients between 2% and 6%. A positive correlation was also observed for beaver colony density and stream gradient in Gatineau Park for gradients ranging from 1% to 10% (Cotton 1990).

In the high coastal plains of South Carolina, Jakes et al. (2007) reported that all of the gradients of all of the streams that were studied were less than 3%. In their case, the optimum gradient was less than 1.2%. The stream gradient was included in the best model to predict the presence of a dam, but its contribution to the relationship remained rather low. Jakes et al. (2007) concluded that the importance of the stream gradient is strongly dependent on topographic variability in the region (Jakes et al. 2007). In relatively flat landscapes, where the stream gradient values are low (<1.5%), the gradient varies little and is not a determining factor in the construction of beaver dams (Barnes and Mallik 1997). In the Abitibi-Témiscamingue lowlands of Québec, Tremblay (2010) also found that the probability of presence of beaver dams on culverts was not related to the stream gradient.

Stream size and depth

Several of the modelling studies that were reviewed revealed stream width to be an important beaver habitat criterion. However, this variable can exert both positive and negative effects (Table 2). The most accurate models for calculating the maximum density of active colonies per river section in Massachusetts (Howard and Larson 1985), and beaver habitat use in the Truckee River basin of Nevada and California (Beier and Barrett 1987), included river width as a predictor variable. In both cases, the relationship between stream width and habitat quality was positive. Conversely, other studies have indicated that stream width has a negative effect on beaver habitat. For example, Suzuki and McComb (1998) noted that the frequency of dams was negatively associated with increasing stream width. Water depth has also been analyzed in some studies (Table 2), but has been identified as significant in only two cases (Beier and Barrett 1987; Dieter and McCabe 1989). A deep stream provides better protection from predators by ensuring that beaver lodge entries are fully submerged, allowing beavers to enter underwater, even during winter (McGinley and Whitham 1985).

According to the analysis of Suzuki and McComb (1998), a strong positive correlation exists between the depth and the width of a stream. On wide, deep streams, beaver dams may not be strong enough to withstand the force generated by large volumes of water during floods (McComb et al. 1990). The cross-sectional area (m^2), which combines the depth and average width of the watercourse, was identified by Barnes and Mallik (1997) as a strong determinant of beaver dam placement in northern Ontario (Table 2).

Watershed size

Several studies have failed to include the size of the watershed. Yet, of the four studies which considered this variable, three stated that watershed size is a significant beaver habitat variable (Table 2). Barnes and Mallik (1997) in Ontario and Jakes et al. (2007) in South Carolina recognized the size of the upstream watershed as the most important factor for determining the presence of a beaver dam. In the upper coastal plains of South Carolina, beavers were more inclined to build dams on rivers the watershed area of which was of medium size (i.e., 1000–5000 ha) (Jakes et al. 2007). On the one hand, Jakes et al. (2007) concluded that small watersheds are inadequate for the establishment of beavers due to the intermittent presence of surface water. On the other hand, excessive water speed and other physical problems that are related to the amplitude of discharge reduce the suitability of the habitat for beavers in large river basins. McComb et al. (1990) did not document the importance of watershed size, but it could be a result of the spatial distribution of

Table 2. The relationship between geomorphological factors and beaver habitat according to selected modelling studies.

Study Code	Response variable	Stream gradient (%)	Stream length (m)	Stream depth (m)	Size of watershed (ha)	Length of floodplain (m)	Substrate type	Riparian slope (%)
1	Number of dams potential sites per section	-	-	ns	n/a	+	n/a	ns
2	Number of potential sites per section	-	-	n/a	n/a	n/a	n/a	n/a
	Number of potential sites per lake	n/a	n/a	n/a	n/a	n/a	n/a	n/a
3	Presence/Absence of dams	-	ns	ns	ns	ns	ns Type of riparian soil	-
4	Presence of colonies (active, abandoned potential sites)	-	+	+	n/a	n/a	n/a	ns
5	Presence/Absence of lodges	n/a	ns	+	n/a	n/a	n/a	-
6	Presence of dams (active, abandoned, unoccupied sites)	ns	-Cross-section of the stream (m^2)		-	n/a	n/a	ns
7a	Density of colonies (per 4 km^2)	n/a	n/a	n/a	n/a	n/a	n/a	n/a
7b	Density of colonies (per 4 km^2)	+ Density of streams with a gradient of 2–6%	ns	n/a	n/a	n/a	n/a	ns
7c	Density of colonies (per 4 km^2)	+ Density of streams with a gradient of 1–10%	n/a	n/a	n/a	n/a	n/a	n/a
8	Presence of dams in culverts	-	ns	ns	n/a	n/a	ns	ns Presence/Absence of a slope < 0%
9	Presence of dams within 200 m from roads	-	-	ns	n/a	n/a	ns	ns Presence/Absence of a slope < 0%
10	Density of colonies	-	+	n/a	+	n/a	+ Poorly drained soil	n/a
11	Presence/Absence of dams	-	n/a	n/a	-	ns	n/a	n/a
12	Number of dams in 25 km^2 plots	-	n/a	n/a	n/a	n/a	Ns Presence of clay/silt	n/a

dams in their study, where 71% of dams were located in only 8% of the watershed area (Barnes and Mallik 1997).

Valley/floodplain width

Three studies have incorporated valley or floodplain width, but only Suzuki and McComb (1998) concluded that it was an important determinant of beaver habitat (Table 2). While most dams were located in 25–30 metre-wide valleys, they recorded no dams in the valleys where widths were less than 10 m. Northcott (1964) also noted that narrow valleys were inadequate for beaver due to dry soil conditions, which are unfavourable for the growth of tree species that were utilized by the beaver, such as poplar (*Populus* spp.), willow (*Salix* spp.), alder (*Alnus* spp.) or birch (*Betula* spp.). Rivers with small floodplains are generally associated with high stream gradients, further diminishing their suitability for beaver colonization (Table 2) (Jakes et al. 2007). Suzuki and McComb (1998) detected a strong positive correlation between the riparian slope and width of the valley.

Substrate type

Substrate type was measured according to several different methods, depending upon the study. Only Howard and Larson (1985) noted its importance for beaver habitat (Table 2). Given that the type of substrate is an indicator of drainage, Howard and Larson (1985) opted to transform the substrate type into drainage classes, which turned out to be one of the most important factors in their model predicting the number of active colonies per kilometre of stream. According to their model, the ideal beaver habitat is a relatively large, low-gradient stream on a very poorly drained soil. However, it is generally accepted that beavers do not typically build dams on rocky substrates (Slough and Sadleir 1977). McComb et al. (1990) found that they could greatly improve the performance of their model by removing rocky sites that were erroneously predicted as suitable habitat.

According to the results of Curtis and Jensen (2004), substrate type was highly correlated with stream gradient. Clay and silt, which are commonly used in the construction of dams, are frequently associated with low river gradients.

Riparian slope

Riparian slope has been tested as a beaver habitat predictor by several authors, but it was significant in only two cases (Dieter and McCabe 1989; McComb et al. 1990) (Table 2). In the study by McComb et al. (1990), riparian slope, together with stream gradient and percentage cover of deciduous trees (Table 3), formed the best model for predicting the site of beaver dam construction, where a gentle slope maximized the quality of site. Riparian slope was also the most important physical variable according to Dieter and McCabe (1989) in the prediction of lodge sites. In contrast to the study of McComb et al. (1990), beaver preferred a steep slope (Dieter and McCabe 1989). In the former study, most beaver lodges that were observed along the Big Sioux River in South Dakota were built partially within the riverbank, rather than completely surrounded by water. The authors therefore assumed that since the lodges generally have multiple underwater entry points, a sharper sloping bank could provide sufficient depth to allow the construction of more than one entry (Dieter and McCabe 1989). In general, a steep riparian slope also allows the beaver to escape predators more easily and to transport woody material with less effort to reach their aquatic habitat (Novak 1987).

Habitat factors associated with food availability

Availability of food

The beaver's diet is diverse, consisting of several types of plants (i.e., graminoids, herbaceous and aquatic plants, shrubs, trees), a variety of species, and different plant parts (i.e., flowers, leaves and rhizomes of aquatic plants, and bark, buds and leaves of woody plants) (Jenkins 1975). This possibly explains why the percentage of non-forest cover was often more influential than vegetation type in landscape-scale studies (Lapointe St-Pierre et al. 2017). Despite being a generalist, the beaver exhibits preferences that are likely related to seasonal and annual variation in the nutritional quality of different species (Jenkins 1979). Beavers typically favour herbaceous rather than woody vegetation when the former are available, while the species and size of the stems that are gathered will vary with the distance from the shore (Jenkins 1980). The dendroecological study of Bordage and Fillion (1988) at Lake George (Quebec) revealed a marked preference for trembling aspen (*Populus tremuloides* Michx.), followed by white or paper birch (*Betula papyrifera* Marsh.) and American mountain-ash (*Sorbus americana* Marsh.). It is evident that when present, trembling aspen is the preferred forage plant species of beavers. They will wander a greater distance from the stream to retrieve it than they will for other species. Based on published literature, Denney (1952) compiled a list of plant species in order of preference by beaver for North America. At the top of Denney's list are trembling aspen, willows (*Salix* spp.), balsam poplar (*Populus balsamifera* L.) and alders (*Alnus* spp.). Gerwing et al.

Table 3. Relationship between factors associated with food availability and beaver habitat according to selected modelling studies.

Code	Response variable	Total canopy (%)	Deciduous tree species cover	Shrub species cover	Aquatic plant cover	Coniferous tree cover	Stem diameter	Percentage without vegetation	Forest fires
1	Number of dams potential sites per section	ns	ns	-	+	ns	n/a	ns	n/a
2	Number of potential sites per section	n/a	+ Shoreline length inhabited by *Populus tremuloides*	+	n/a	n/a	n/a	n/a	n/a
	Number of potential sites per lake	n/a	+ Shoreline length inhabited by *Populus tremuloides*	+	n/a	n/a	n/a	n/a	n/a
3	Presence/Absence of dams	ns	+	ns	ns	ns	n/a	n/a	n/a
4	Presence of colonies (active, abandoned potential sites)	n/a	ns	ns	ns	ns	n/a	ns	n/a
5	Presence/Absence of lodges	+	+ Horizontal cover of 1 and 2 m from the ground	n/a	n/a	n/a	n/a	n/a	n/a
6	Presence of dams (active, abandoned, unoccupied sites)	n/a	ns	ns	n/a	ns	+ 1.5–4.4 cm	n/a	n/a
7a	Density of colonies (per 4 km^2)	n/a	+ Young and regenerating	ns	n/a	ns	n/a	n/a	+
7b	Density of colonies (per 4 km^2)	n/a	+	ns	n/a	ns	n/a	ns	ns
7c	Density of colonies (per 4 km^2)	n/a	ns	ns	ns	ns	n/a	n/a	n/a
8	Presence of dams in culverts	n/a	ns Distance from the culvert	ns	n/a	n/a	n/a	ns	n/a
9	Presence of dams within 200 m from roads	n/a	ns Distance from the culvert	n/a	n/a	n/a	n/a	-	n/a
10	Density of colonies	ns	+	ns	ns	ns	n/a	ns	n/a
11	Presence/Absence of dams	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
12	Number of dams in 25 km^2 plots	n/a	Hardwood cover ns	Alder cover-	n/a	n/a	n/a	-	n/a

Significant variables (+ positive effect, – negative effect), non-significant variables (ns) or unanalyzed variables (n/a).

(2013) reported that among nine plant species examined, beavers selected three willow species (*S. scouleriana, S. drummondiana, S. sitchensis*) and were able to differentiate among closely related species. Nevertheless, beavers can occupy areas in which preferred species are absent (Jenkins 1975) and they are capable of surviving in coniferous areas (Brenner 1962). The importance of aquatic vegetation in beavers' diet in those areas has not yet been determined.

All of the studies that we reviewed measured one or more factors that were related to food availability. Deciduous tree cover is the most frequently quantified variable and it appears to be positively related to beaver habitat in six of the 12 studies that were examined. However, studies where the response variable was colony rather than dam apparently placed greater emphasis on this predictor variable (Table 3). Such a result probably stems from the fact that dams are constructed to increase the surface area of the stream and to bring beavers closer to the food on the shore, together with providing protection from predators and disturbances. Thus, high quality habitat and habitat that beavers may select could be habitats where they do not need to build a dam. Using the preferred vegetation list that was assembled by Denney (1952), Slough and Sadleir (1977) measured the length of shoreline that was dominated by aspen and willow. This variable was the most significant predictor in their model of the number of potential sites per lake for beaver. Cotton (1990) also found that deciduous vegetation cover was positively correlated with the density of beaver colonies for two of her three study regions in Quebec. In a system that was dominated by grasslands along the Big Sioux River in South Dakota, Dieter and McCabe (1989) identified the vegetation cover 0–2 m from the ground as an important factor for the selection of beaver lodge sites.

In subarctic environments, beavers occupying ponds eat more aquatic vegetation (e.g., variegated pond-lily *Nuphar variegata* Engelm. ex Durand) in winter than beavers occupying streams, which eat more terrestrial shrubs. For example, on the territory of the Wemindji Cree First Nation in eastern James Bay (Quebec), beaver diets were comprised of 60–80% aquatic vegetation (Milligan and Humphries 2010).

According to Jenkins (1980), the opportunistic nature of beavers could diminish the importance of habitat variables that are related to food compared to physical and hydrographic factors. Collins (1976) noted few abandoned territories where food resources were depleted. Moreover, he estimated that the potential density of colonies in northwestern Wyoming was limited primarily by the availability of water, followed by the distribution of preferred food species. Similarly, several studies including those of Barnes and Mallik (1997) in Ontario, Beier and Barrett (1987) in Nevada and California, Howard and Larson (1985) in Massachusetts, and McComb et al. (1990) in Oregon, concluded that the presence of food resources is not the most important factor in selecting suitable beaver dam sites. Howard and Larson (1985) suggested that a relationship exists between physical factors and food availability; the availability of woody species is of secondary importance, except during the initial stages of occupation, when they serve as building materials for dams. Beavers alter riparian plant community composition by removing certain species, thereby stimulating the growth of non-preferred species (Barnes and Dibble 1988). Although little information can be gathered regarding vegetation community composition prior to beaver establishment (Beier and Barrett 1987), studies that have used ground-penetrating radar suggest that some sites may be used repeatedly for prolonged periods of time (Kramer et al. 2012). According to Barnes and Mallik (1997), flooding following dam construction generally facilitates the growth of a high density of herbaceous plants. Models that are based on physical factors, with or without the inclusion of vegetation variables, can explain much of the variance among suitable and unsuitable dam sites. These models could predict establishment of colonies and the duration of occupation, whereas models including only vegetation variables were unable to make these predictions (Howard and Larson 1985; Beier and Barrett 1987; Suzuki and McComb 1998).

Finally, the degree of habitat stability in Cotton's (1990) three study areas is reflected in which variables best described the variation in observed beaver density. In mature hardwood forests, the availability of food was rather stable and, therefore, hydrographic variables explained most of the variation in colony density (Cotton 1990). In contrast, variables that were related to vegetation were the most significant on the north shore of the St. Lawrence River, where food availability varied as a result of numerous disturbances. Similar regional variations were also observed by Lapointe St-Pierre et al. (2017) using the number of dams.

Tree-stem diameter

Slough (1978) observed that some woody plants, such as alder, are harvested by beavers for the construction of dams rather than being utilized as a food source. The use of woody stems for shelter or food appears to depend upon stem diameter rather than upon species (Barnes and Mallik 1996). In southern Algonquin Park, Ontario, cut stem diameters averaged 15.1 cm, with a maximum of 45.3 cm, and the number of stems that were cut declined sharply with increasing distance from water (Donkor and Fryxell 1999). Small stems of speckled alder (*Alnus incana* subsp. *rugosa* [Du Roi] R.T.Clausen) were abundant near the shoreline and are easily cut by beavers, thereby providing the resources that are required for quick dam construction as well as minimizing the amount of time spent on the shore where beavers risk encountering predators (Barnes and Mallik 1996). No other authors considered tree diameter to be a determinant of suitable beaver habitat, which possibly stems from the fact that studies examined sites that were occupied for different periods of time. However, Barnes and Mallik (1997) argued that beavers establish dams in stream segments containing a high density of woody riparian vegetation, with stem diameters ranging from 1.5 to 4.4 cm, within the first 10 metres from the shoreline (Table 3).

Forest fires

Of the reviewed studies, the effect of forest fires on beaver habitat was considered in only one case. In Cotton's (1990) beaver habitat model for the North Shore of the St. Lawrence River, the area that had been burned was among the variables describing the density of colonies, because natural disturbances such as catastrophic wildfire predominate in the boreal forest compared to the other study areas (Table 3). While forest fires cause a short-term decrease in food availability, beaver density increases sharply during the first 10–30 years following fire (Cotton 1990). The reason for this is that in boreal forest, disturbances such as fire and logging often facilitate the establishment of trembling aspen, which improves beaver habitat quality (Slough and Sadleir 1977; Cotton 1990; Potvin and Breton 1997). Although forest fire dynamics are assumed to be beneficial for beavers (Naiman et al. 1988), the benefits depend upon several factors, such as the frequency and severity of forest fires, herbivory and drought (Hood et al. 2007).

Potvin and Breton (1997) and Brunelle et al. (1989) observed that logging practices, which aim to protect natural regeneration, have a minor effect on the abundance of beaver colonies. Five years after harvest, beaver densities were two to three times greater than in undisturbed forest (Brunelle et al. 1989). Defoliating insect outbreaks may also produce favourable results for beaver by facilitating the growth of young trees (Cotton 1990).

Habitat factors associated with anthropogenic infrastructure

Culverts and roads are often utilized by beavers as foundations for dams, which can maximize potential flooding with minimal construction effort (Jensen et al. 2001). Generally, forest managers must systematically remove beaver dams from culverts in order to maintain roads and prevent damage to infrastructure (Flynn 2006).

Jakes et al. (2007) found that the presence of a road crossing on a stream was significantly associated with the probability of dam presence. Beavers were more inclined to install dams on low gradient (≈ 0.6–1.2%) stream segments containing a road crossing, and that were located in a watershed about 2500 ha in size. Flynn (2006) specifically studied the spatial association between beaver ponds and culverts in Alberta. She detected a positive effect of culvert proximity on the occurrence of beaver ponds, but these results were restricted to a 300 m scale and to second-order streams. In general, the areas that were flooded by beaver were not associated with the presence of a culvert, but strongly related to other variables, such as stream gradient, proportion of deciduous forest or stream order. Similarly, McComb et al. (1990) found that the distance from infrastructure did not vary between occupied and unoccupied sites.

Factors that determine whether or not a culvert would be blocked by beavers have been studied by Jensen et al. (2001) in Upstate New York. The size of the culvert was the most influential variable, followed by the stream gradient. Culverts with small diameters constrict water flow and increase the velocity of the moving water. Beavers are attracted to the culvert by the sound of running water (Novak 1987). In another study in the same area, the proportion of land devoid of woody vegetation within 200 m of the road emerged as the most influential variable for predicting beaver presence (Curtis and Jensen 2004). The gradient and width of the stream were also important variables that were included in the model. According to their results, the environment along a highway in Upstate New York has little chance of being colonized by a beaver where the stream gradient exceeds 3% and when over 50% of the area is devoid of woody vegetation. The availability of food, however, does not appear to be a good predictor of beaver occupancy near roads (Jensen et al. 2001). Martell (2004) noted that beavers forage significantly less near roads despite a similar forest composition; the author concluded that beavers do not use road borders in the same way they use forest interior.

Discussion

After reviewing 12 major modelling studies of beaver habitat in North America, we found that the identification of key beaver habitat varies depending upon: 1) geomorphological characteristics of the region; 2) the nature of the response variable (beaver dam or colony); and -3) the scale at which the study is conducted (Figure 2). Regarding the last point, efforts have been particularly invested in models and studies at local scales.

Several variables were analyzed in different models and, more importantly, considerable variability exists among these models regarding which environmental factors are the most influential predictors. Despite this variability, the stream gradient emerged as one of the most important factors in the studies that were examined in this article (Table 2). All the authors agreed that habitat quality decreases as the stream gradient increases. On its own, this variable is insufficient for predicting site quality for a beaver dam (McComb et al. 1990). As McComb et al. (1990) explained, the relationship between the construction of a dam and the stream gradient could be influenced by the cross-sectional area of the stream. Barnes and Mallik (1997) also identified stream cross-sectional area as an instrumental variable for predicting beaver dam establishment.

While the breadth and depth of streams are often noted as important variables, the interpretation of the relationship between these variables and beaver habitat quality varies between studies. Furthermore, these factors may be highly correlated with one another (Suzuki and McComb 1998). For the purposes of modelling, Jakes et al. (2007) suggested that the size of the watershed is an effective substitute for stream width or depth, which directly influences beaver dam establishment. Other geomorphological factors, including slope and shoreline substrate, are not decisive variables for beaver habitat, based upon the 12 beaver habitat-modelling studies that are presented in this review. The importance of these secondary variables is relative to the regional context. Thus, Dieter and McCabe's (1989)

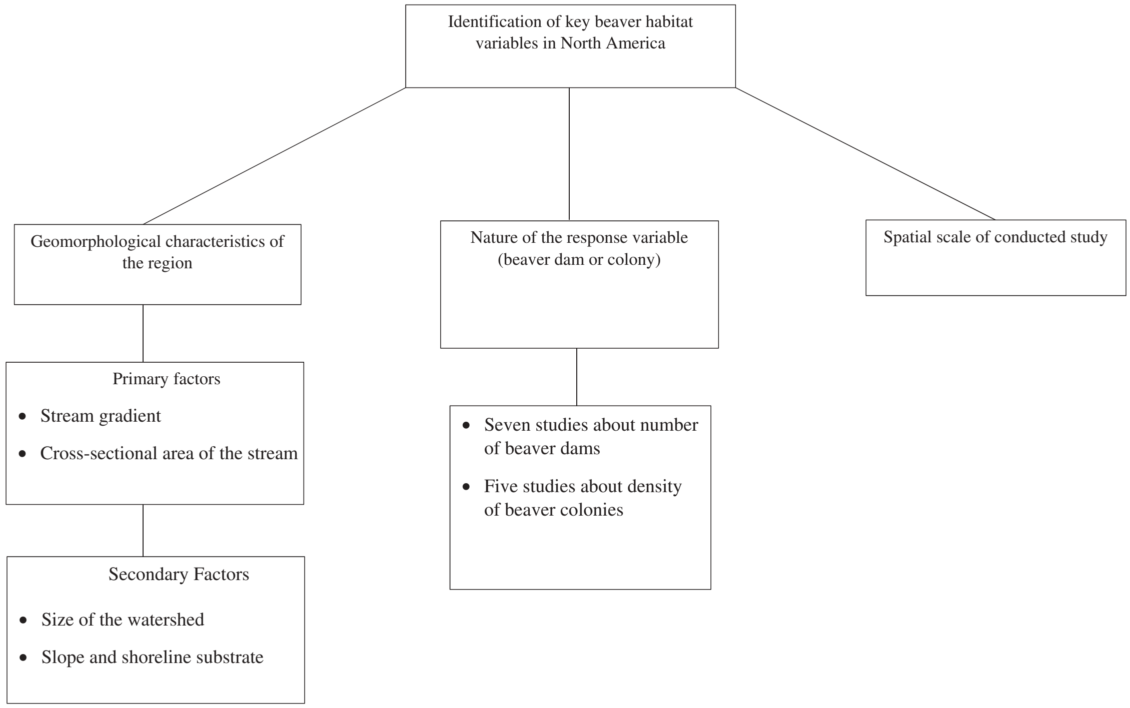

Figure 2. Identification of key beaver habitat in North America based upon 12 reviewed studies.

observations of lodges that were built directly into the riverbanks in the Dakotas appear to be an exceptional case.

The importance of beaver habitat factors that are associated with food availability (Table 3) remains ambiguous. Researchers do not always take into consideration the vegetation at the study site prior to the construction of dams or establishment of beaver colonies. Suzuki and McComb (1998) acknowledged that a lack of records for vegetation that existed prior to beaver occupation could explain the poor predictive ability of the vegetation variables in their model. In contrast, Barnes and Mallik (1997) sampled vegetation types that were present before beaver dams were constructed. They concluded that vegetation was an important factor, but only in relation to stem diameter. These results are consistent with those of Howard and Larson (1985), suggesting that woody stems are mainly important at the onset of beaver occupation, when they are used as building materials.

Howard and Larson (1985) also addressed an important element of the relationship between geomorphic habitat factors and food availability (Howard and Larson 1985; Beier and Barrett 1987; McComb et al. 1990). The authors argued that if beavers occupying more southerly latitudes continue to feed upon aquatic plants during the winter, the hydrologic habitat factors that are associated with sufficient vegetation production during the summer growing season should significantly influence the availability of food during winter (Howard and Larson 1985). They strongly recommended the inclusion of a measure of herbaceous food availability in models for regions where beavers do not collect and store woody food reserves for the winter. In contrast, in northern regions, the availability of woody material should have greater importance. Nevertheless, the authors maintained that further studies are needed to determine if northern beavers rely upon aquatic vegetation under the ice, in order to estimate the relative importance of herbaceous and woody vegetation as winter food resources.

It is difficult to draw conclusions about the effect of infrastructure upon the selection or use of habitat by beavers. Only three studies have considered infrastructure, such as roads, in their models (McComb et al. 1990; Jakes et al. 2007; Lapointe St-Pierre et al. 2017); their conclusions differ. The presence of roads significantly improved the model prediction of dam locations in Jakes et al. (2007), whereas McComb et al. (1990) and Lapointe St-Pierre et al. (2017) did not observe such an effect. According to McComb et al. (1990), beavers colonize an area adjacent to human infrastructures only when all necessary habitat factors are present. As is the case in regions that are undisturbed by humans, these habitat factors include stream gradient and width (Jensen et al. 2001; Curtis and Jensen 2004). While food availability is not always a determining factor in beaver habitat models, a roadside that is largely devoid of woody vegetation tends to decrease the habitat quality of the surrounding area (Curtis and Jensen 2004), which was also shown to be a good predictor of dam abundance at the scale of 25 km^2 plots (Lapointe St-Pierre et al. 2017). The removal of deciduous cover near logging roads, which is used as a preventive control over beaver occupation, should be practiced with caution given its potential impacts on stream bank stability, organic matter inputs and temperature regulation within the stream (Flynn 2006).

Some authors have argued that predictive models of beaver habitat should be developed on a case-by-case basis and regions with dissimilar geomorphology should be analyzed separately (Barnes and Mallik 1997; Suzuki and McComb 1998; Jakes et al. 2007). The results of our literature review, however, did not reveal a clear distinction between regions with regard to important environmental variables and their relationships with beaver habitat. It is interesting to note that in models where the response variable was related to beaver dams, the explanatory variables were mostly geomorphological habitat characteristics (Table 2). Only the model of McComb et al. (1990) includes hardwood cover (Table 3). Barnes and Mallik (1997) also showed that small stem diameter was significant, but this was in reference to woody plants as a source of dam-building materials rather than as a food resource. The importance of habitat variables that were associated with food availability was identified primarily by studies that modelled beaver colonies. The characteristics of riparian vegetation usually require field sampling and, therefore, are more difficult to incorporate into predictive models that are developed for large areas (Jakes et al. 2007; but see Lapointe St-Pierre et al. 2017).

As mentioned previously, most models that are developed at the local level require data collection in the field. This is a costly exercise in terms of both time and money, which does not encourage their use in contexts of forest, land or wildlife management. Today, the availability and quality of population and environmental data in a digital format, coupled with increasing access to advanced GIS tools, allows beaver habitat to be modelled spatially over large territories. As an example, Lapointe St-Pierre et al. (2017) were recently able to model abundance of beaver dams at the scale of forested regions of the Province of Quebec (>300,000 km^2) using only remotely sensed data. Given the ecological impact of beavers and their ability to modify species composition in wetlands and riparian ecosystems for taxa as diverse as plant (Hood and Bayley 2009), fish (Collen and Gibson 2000), waterfowl (Rempel et al. 1997) or other waterbird communities (Nummi and Holopainen 2014), and also ecological processes such as carbon sequestration (Moore 1999), it is quite appropriate that future studies should aim to develop reliable and applicable predictive spatial models using stream gradient and forest cover types. These models would allow the management of beaver habitat across vast areas. For example, maps that are developed at the watershed scale or for geomorphologically homogeneous areas, which indicate wetlands currently or potentially occupied by beaver, would have valuable applications in the management of forests, land and wildlife.

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