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Factors affecting site selection by beavers colonizing streams in the upper Midwest region of the United States

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Abstract

Beaver management requires understanding beaver habitat preferences. Despite the American beaver (*Castor canadensis* Kuhl, 1820) being relatively common in the upper Midwest region of the United States, there are no beaver habitat relationship models based on this area. We used 1735 colonization events from long-term monitoring data generated by the Chequamegon-Nicolet National Forest in northern Wisconsin, USA, to determine what geomorphological and biological factors were selected by beavers colonizing new sites. We developed and evaluated prediction performance for three colonization models: geomorphology factors only, geomorphology and vegetation factors, and a full colonization model based on geomorphology, vegetation, and availability of dispersing beavers. Overall, the geomorphology–vegetation–colonizer model was the best model, predicting actual colony locations better than the other two models. Spatially, the landscape open to beaver colonization was a mosaic of streams with suitable and unsuitable habitat. These models improve our understanding of how beaver site selection factors in the upper Midwest region differ from factors identified in the literature for the western and eastern United States. This information may be useful for land managers in this region seeking to spatially target resources for restoring northern forest landscapes such as the Chequamegon-Nicolet National Forest.

Key words: beaver, *Castor canadensis*, colonization, habitat model, site selection, occurrence

Introduction

The American beaver (*Castor canadensis* Kuhl, 1820) was widely distributed across North America, but after European settlement, it experienced precipitous declines across its geographic range due to habitat degradation and overexploitation (Naiman et al. 1988). Since the 1920s, reintroduction efforts and stricter hunting regulations yielded a successful rebound in the population, with beaver populations returning to many formerly extirpated areas (Naiman et al. 1986). Approximately 6–12 million beavers are now present in North America, and they have adapted well to anthropogenically modified landscapes (Naiman et al. 1988).

While recovery of the American beaver has been deemed a success story in wildlife management, the relationship between humans and beavers is often competitive. As beaver populations continue to rebound, land use preferences between humans and beavers are often misaligned, leading to human–wildlife conflict (Jonker et al. 2006; Siemer et al. 2013). For example, in the eastern and midwestern United States, beavers are often thought to have deleterious effects on recreational cold-water fisheries (Collen and Gibson 2001; Johnson-Bice et al. 2018) due to beaver dams slowing water movement, which may allow stream waters to warm beyond the preferences of economically desirable cold-water fish. In other types of streams, however, there is interest in maintaining a sustainable beaver for harvest and to obtain the benefits of beaver ecosystem engineering. Balancing these competing objectives (e.g., Wisconsin Department of Natural Resources 2015) requires a robust understanding of beaver habitat requirements and preferences.

Despite beavers being relatively common in the upper Midwest region of the United States, there are no beaver habitat relationship models based in this area (Touihri et al. 2018); the closest study found by Touihri et al. (2018) was in the Great Plains of the United States in the relatively dry grasslands of South Dakota (Dieter and McCabe 1989). Beaver management in Wisconsin (Wisconsin Department of Natural Resources 2015) provided us the opportunity to remedy this lack. As part of beaver management in northern Wisconsin, the Chequamegon-Nicolet National Forest's (hereafter CNNF) management plan for sustaining its cold-water fishery involves removal of all beaver colonies established on high-value cold-water trout streams during the early spring (Ribic et al. 2017). This means that every spring, many kilometers of stream habitat are unoccupied and awaiting potential beaver colonization by dispersing beavers from other streams. Given the lack of regional beaver habitat relationship models for the upper Midwest region of the United States, creating such a model would serve as a bridge between models developed for the west and east (reviewed in Touihri et al. 2018), as well as potentially provide useful land management information.

A number of studies outside of the region of interest have focused on understanding habitat and stream characteristics that influence beaver site selection (e.g., Hallett and Erickson 1980; Howard and Larson 1985; Barnes and Mallik 1997; Cox and Nelson 2009). In their review of published beaver habitat models, Touihri et al. (2018) concluded that the selection factors were primarily stream gradient, size of watershed, and hardwood cover that is adjacent to the streams. However, each modeling study reported finding significant explanatory variables not identified in other studies. Touihri et al. (2018) conjectured that this might reflect differences in the variables measured and how they were measured, and whether colonies or dams were the unit of measure. In addition, they pointed out that in the 12 models, they found describing beaver-habitat relations across North America, and the differences in the relationships could be traced to differences in ecoregion characteristics (e.g., stream characteristics, geomorphology, etc.). That is, globally, beavers may have a nonlinear response to a particular site characteristic that simply appears to be positive or negative in regional studies that are exposed to relatively small windows of the variable's total domain. This variability in response emphasizes the potential usefulness of a model tuned to the characteristics of the under-studied upper Midwest region. Such a model would improve our scientific understanding of beaver habitat relations across the beaver's range and allow beaver management in the region to be based on an appropriate set of habitat relations.

Emphasizing how variable beaver habitat relations appear to be across their range, Touihri et al. (2018) reported that 4 of the 12 habitat models found no significant relationship with the vegetation variables used. While this may appear to be illogical—suitable availability of food resources is, after all, a requirement for a successful beaver colony—there are at least two ways to understand the result. The most obvious perspective is that the four unusual studies were simply not measuring the relevant vegetation variables. However, it is also possible that in those study areas, the food resources were always sufficiently abundant for these food generalists that food availability was not a discriminating factor for the beavers. Dittbrenner et al. (2018) took this idea of there not being a strong relationship with vegetation a step further to develop a "beaver intrinsic potential" (BIP) model for the Snohomish River Basin (~4807 km^2) in the state of Washington. Because of the "intrinsic potential" focus, their model considered only factors that a beaver colony could not alter. The resulting model used stream gradient, valley width, and stream width. This aligned well with Touihri et al.'s (2018) conclusion that stream gradient, watershed size, and hardwood cover were primary factors; given the geomorphology conditions in Dittbrenner et al.'s (2018) study area, watershed size and valley width are likely to be highly correlated. The Dittbrenner et al. (2018) model was powerful enough in successfully categorizing habitat occupancy by beaver to warrant consideration of this approach for our study area. Furthermore, as both Dittbrenner et al. (2018) and Jakes et al. (2007) observe, purely geomorphological models are attractive because the relevant variables are readily obtainable from remote sensing data sources.

We used the long-term monitoring data generated by the CNNF to determine what geomorphological and biological factors were selected by colonizing beavers in this upper Midwest region. Our objectives were to (1) develop a hierarchical set of regional colonization models based on geomorphology, vegetation, and beaver behavior; (2) compare how these models performed relative to each other and to models based on other parts of the beaver's range; and (3) assess whether these regional models provide useful insight into local beaver management options.

Methods

Study area

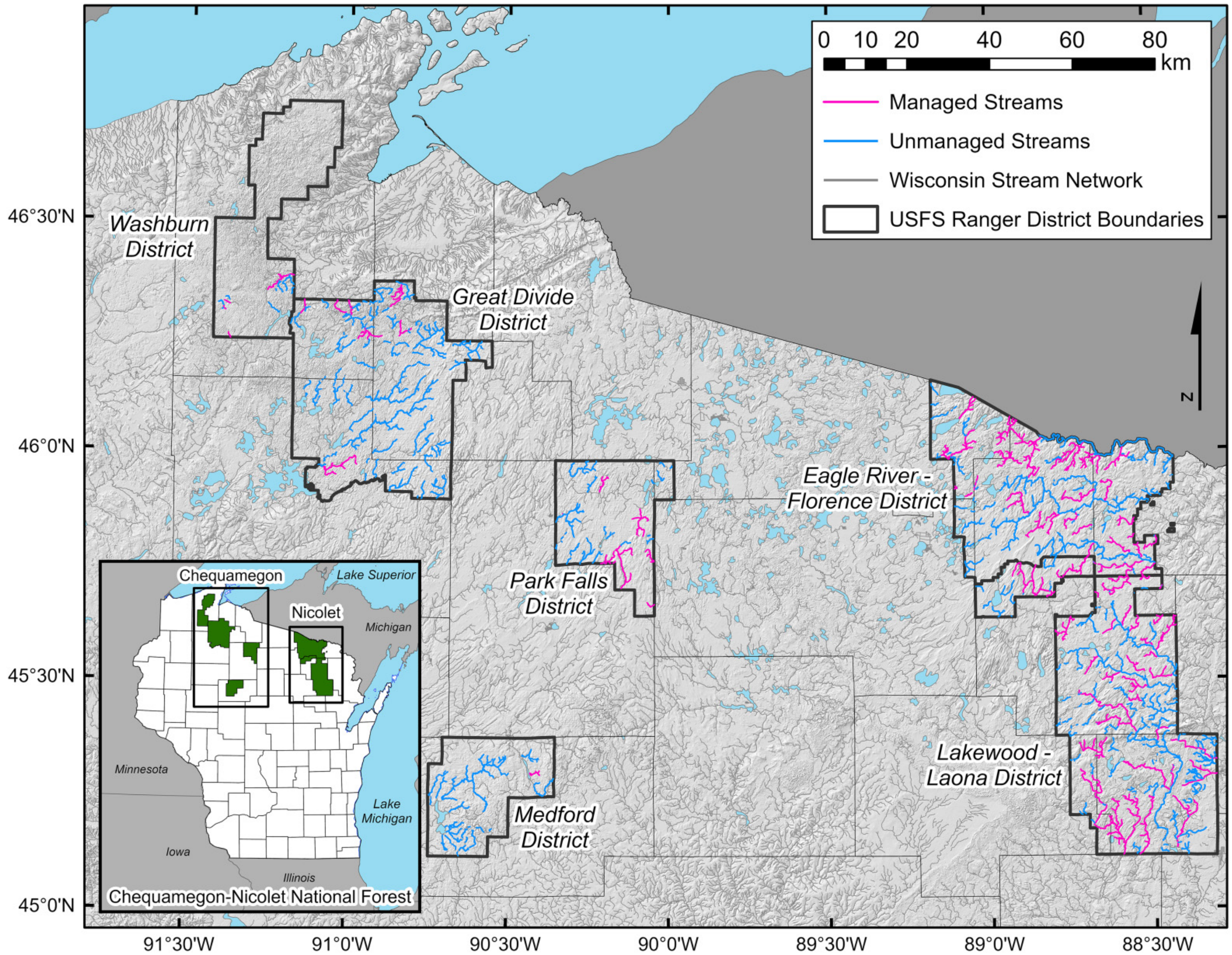
The CNNF is located in northern Wisconsin; the Chequamegon side (~3474 km^2) of the forest is in northwestern Wisconsin; the Nicolet side (~2676 km^2) is in northeastern Wisconsin (Fig. 1). The Chequamegon side contains large tracts of contiguous National Forest land while the Nicolet side is more interspersed with private lands. Hydrologically, the CNNF holds mainly headwater streams; >80% of streams are narrower than 15 m and are rated as Strahler stream order 1 or 2 (Ribic et al. 2017). Wisconsin stream segments are categorized by a three-class system based on trout suitability (Wisconsin Department of Natural Resources 2023). Class 1 denotes high-quality trout streams with natural reproduction, Class 2 are moderate quality trout streams supporting limited natural reproduction, but which rely on annual trout stocking, and Class 3 are marginal habitat for trout that do not support any natural reproduction and must be stocked annually.

The CNNF is embedded in a landscape that has been scoured by repeated glaciation cycles, leaving little topographic relief with flat landscapes and occasional gently rolling hills (Stevens et al. 2001). The forest is classified as a Laurentian mixed forest ecosystem (McNab and Avers 1996). Predominant forest and vegetation types consist of large tracts of conifers [northern white cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), pine (*Pinus* spp.), spruce (*Picea* spp.), tamarack (*Larix laricina* (Du Roi) K. Koch)], and deciduous trees [aspen (*Populus* spp.), paper birch (*Betula papyrifera* Marsh.), black ash (*Fraxinus nigra* Marsh.), basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), maple (*Acer* spp.), oak (*Quercus* spp.)], and shrubs [alder (*Alnus* spp.), willow (*Salix* spp.)].

Colony location data

Beaver management in the CNNF is provided by the US Department of Agriculture's Animal and Plant Health Inspec-

Fig. 1. Map of the Chequamegon-Nicolet National Forest in northern Wisconsin, USA, showing the stream network and which streams experienced American beaver (*Castor canadensis*) management designed to improve stream condition for use by cold-water trout. Map projection is NAD 1983 HARN Wisconsin TM (meters). The map has five components: state boundaries (National Atlas of the United States 2013*b*), inland waters (National Atlas of the United States 2013*a*), Wisconsin county boundaries (Wisconsin Department of Natural Resources 2017*a*), Wisconsin stream network (Wisconsin Department of Natural Resources 2017*b*), and Wisconsin hillshade model (Wisconsin Department of Natural Resources 2019).



tion Service (USDA-WS). The management protocol has two distinct phases (Animal and Plant Health Inspection Service 2012). The intensive removal phase resulted in lethal removal of all beavers and removal of all dams, including older dams that were revealed as newer dams were removed and water levels declined. This was accomplished by repeatedly walking the managed streams to ensure complete removal; this phase can take two to four years (Animal and Plant Health Inspection Service 2012). The maintenance phase uses a two-part protocol. Yearly aerial surveys were flown in the fall over all streams within the CNNF to locate active beaver colonies. The surveys were conducted after leaf-off in mid-October–November by experienced observers in a light aircraft flying 213–244 m above the surface at 128–161 km/h (Ribic et al. 2017). Colonies were considered active if there was a dam or lodge with fresh mud or cuttings and (or) a food cache with fresh cuttings. In this region, it is very rare for active beaver colonies on streams to not have a dam or, during fall, an active food cache. Active beaver colonies and structures were removed on those stream segments targeted for management, primarily Class 1 and Class 2 streams; some Class 3 streams were also managed because of their proximity to Class 1 or 2 streams. Removals were done by USDA-WS in April to early May each year following the fall survey (Dickerson 1989; Animal and Plant Health Inspection Service 2012). Land management actions were conducted using best management practices per USDA-WS directives (Animal and Plant Health Inspection Service 2014) and are not subject to IACUC review. Due to the thoroughness of this management protocol, there was very high confidence that dispersing beavers encountered an entirely uncolonized landscape of managed streams and that the vegetation on those streams had not been materially affected by beaver efforts at ecosystem engineering.

The maintenance phase of beaver management began in 1987 on the Nicolet side and 1997 on the Chequamegon side of the CNNF. Colony locations from the 1987–2014 aerial surveys were used for our analyses. All active colonies were marked on a map and later digitized into an ArcGIS Pro 2.8 (Esri 2021) geodatabase; beaver locations were accurate to within 15 m of a stream (median of 1773 observations; interquartile range = 0.6–40 m). Beaver colonization events were defined by each year's new colony locations on managed streams. We used only colonization events that occurred in permanent streams. While colonization events can occur in intermittent streams, such colonies are not sustainable (Novak 1987). Colony territories were represented as virtual boxes in the ArcGIS Pro geodatabase. The sides extended 100 m lateral to the stream (Howard and Larsen 1985). One end of the box was placed at the digitized colony location and the other end placed 150 m upstream, for a total area of 3.0 ha. The size of the core area box is comparable to core areas of unexploited beavers in Illinois streams (Slough and Sadleir 1977; Bloomquist et al. 2012). Because colonizing beavers experienced a "blank slate" every year on managed streams, they were able to repeatedly select particular sites (or sites near to previously selected sites).

With the beaver presence sites identified, we used ArcGIS Pro to fit points along the river polylines every 150 m, place core area boxes at each point, and then delete any box that overlapped with a beaver territory box. This process defined a set of sites that were never colonized by beavers during the observation period.

Site variables

There was no reason to believe that beavers in this region used an entirely different set of factors in selecting sites than beavers studied outside of the region. There was reason to believe that the nature of the relationships and their relative strength would be different. Therefore, we used geomorphology and vegetation variables that were related to or similar to the important variables of Dittbrenner et al. (2018) and Touihri et al. (2018). The geomorphology variables considered were stream width, stream temperature, stream alkalinity, stream water source, stream gradient, watershed size, valley relief, and soil drainage. The vegetation variables were land cover proportions of deciduous trees (aspen and hardwoods), coniferous trees, and lowland (i.e., near the stream) shrubs.

Stream width class, temperature class, alkalinity class, and water source were taken from the CNNF's geodatabase. Stream width categories were narrow (<6 m), medium (6–15 m), and wide (>15 m). Stream temperature categories were cold (<23 °C), cool (23–26 °C), and warm (>26 °C). Stream alkalinity class categories were acid (<5 mg/L $CaCO_3$), neutral (5–20 mg/L $CaCO_3$), and alkaline (>20 mg/L $CaCO_3$). Water source categories were groundwater and surface. Stream gradient was calculated by assessing the change in elevation between the presence or absence point and the point 150 m upstream where the core area box intersected the stream; elevations were obtained from the National Elevation Dataset (U.S. Geological Survey 2002). Watershed size was obtained from the National Watershed Boundary Dataset (U.S. Geological Survey 2016) using the areas associated with the hydrologic unit code 12-digit codes.

Valley width was defined in Dittbrenner et al. (2018) as the average width of the area adjacent to a stream segment that was within 2 m vertical elevation of the channel elevation. Dittbrenner et al. (2018) found the optimal valley width to be 30 m and cited previous work in the western U.S. that had found it to be 46 m. Due to the relatively low topographic variability of our study area, valley width was not likely to be informative. We used a related variable, defining "valley relief" as the average elevation 40 m from the presence or absence point relative to the elevation of the presence or absence point. The 40 m radius was a compromise between the two western U.S. optima of 30 and 46 m reported by Dittbrenner et al. (2018). We computed valley relief in ArcGIS with elevation data obtained from a 0.6 m LiDAR-based digital elevation model (DEM) (Wisconsin Department of Natural Resources 2019).

The ability of a beaver dam to accomplish its function of flooding the upstream area depends in part on the permeability of the streambed material, which has been found to be an important variable in previous beaver habitat modeling (Howard and Larson 1985). Following Howard and Larson (1985), we used the ordinal soil drainage classification maintained by the Soil Survey Geographic Database (SSURGO) (U.S. Department of Agriculture 2019). The drainage class with the highest percentage within each core area box was considered the predominant drainage type for that point. There were seven SSURGO categories ("excessively drained", "somewhat excessively drained", "well drained", "moderately well drained", "somewhat poorly drained", "poorly drained", and "very poorly drained") in the drainage class variable. Howard and Larson (1985) found that the probability of beavers colonizing a site decreased as soil drainage capability increased. However, because the beavers might not be responding linearly to the changes in classes (as assumed by Howard and Larson 1985), we considered two simplified categorizations of drainage class. The first was a two-category drainage variable composed of poor drainage (SSURGO categories "poorly drained" and "very poorly drained") and better drainage (the other five SSURGO categories). The second was a three-category drainage variable that retained poor drainage (SSURGO categories "poorly drained" and "very poorly drained") and divided better drainage into moderately good drainage (SSURGO classes "well drained", "moderately well drained", and "somewhat poorly drained") and very good drainage (SSURGO categories "excessively drained" and "somewhat excessively drained").

For the vegetation variables, we used periodic CNNF forest inventories that are conducted every three years, with the data maintained in a set of databases. The databases contain vegetation information, in vector format, related to the total area and predominant tree species or vegetation type for each forest management unit. We condensed forest cover and tree species information into vegetation categories to best represent vegetation communities useful as food resources or construction materials for beaver; these vegetation classes were deciduous trees (aspen and hardwood), coniferous trees, and lowland shrubs. Vegetation measurements were calculated as the % of each cover class contained in the core use box. Presence points were assigned cover class values based on the most recent forest inventory; absence points were assigned a random habitat year, and then assigned cover class values based on the most recent forest inventory for the assigned year. Because the CNNF did not have a substantial timber removal program during the observation period, vegetation cover changed minimally across the forest inventories.

Colonization sources

Regardless of the attractiveness of a site's geomorphology and vegetation features, a beaver cannot colonize that site if it is not able to arrive at the site to evaluate it. Dispersal from natal colonies, primarily by two-year old young, is a large contributor to colonization events (Sun et al. 2000; McNew and Woolf 2005). In this system, source colonies are on unmanaged streams. On the Chequamegon side of the Forest, beaver colony density on unmanaged streams was stable at approximately 0.22 colonies/km during the period of observation (Ribic et al. 2017). In contrast, the Nicolet side of the Forest started at approximately 0.22 colonies/km but over the course of the observation period declined to approximately 0.08 colonies/km. Given the low/declining beaver density, the probability of colonization seemed likely to be related to the availability of source colonies.

Movement distances for dispersing beaver in previous studies have reported an average between 8 and 16 km (Beer 1955; Leege 1968) with distances up to 238 km recorded (Hibbard 1958). Dispersal distances in beavers, as with most organisms, are skewed right (Sun et al. 2000), i.e., there is a long right tail in the distribution of dispersal distance. Consequently, we used two measures of source colony availability: the number of colonies on streams not targeted for management that were within a circle centered on the colony or absence point using a radius of the median beaver straight-line dispersal distance and the number of colonies on unmanaged streams that were within a circle with a radius of the 75th percentile of the straight-line dispersal distance distribution. There are few studies that provide full dispersal distance distribution information. We used straight-line distances from 200 beaver dispersal events in Wisconsin (Knudsen and Hale 1965) to determine an estimated median dispersal distance of 4.9 km and a 75th percentile distance of 11.3 km.

Statistical analysis

We used logistic regression and information theoretic methods (AIC$_c$; Burnham and Anderson 2002) to develop the beaver colonization models. Because we were interested in how well the models predict colonization, we fit the models using a training set and made predictions with a test set. We used a random selection of 80% of the data as the training set with the remaining 20% being used as the test set.

Model development (training set)

We modeled beaver colonization in four phases. In the first phase, we investigated which drainage class variable fit the data the best by modeling beaver colonization as a function of the individual drainage class variables (two, three, or seven drainage classes). We ranked the models using AIC$_c$ and used the drainage class variable from the model with the minimum AIC$_c$ value as the best drainage class variable to use in subsequent modeling. The next three phases modeled beaver colonization using geomorphology variables only; geomorphology and vegetation variables; and geomorphology, vegetation, and colonizers. In the second phase, we determined the best geomorphological model using the following variables: stream gradient, drainage class, water source, stream width, stream alkalinity, stream temperature, valley relief, and watershed area. The geomorphology model set was all combinations of the geomorphology variables, as there were no collinearity issues in that set of variables. In the third phase, we added the vegetation variables to the best geomorphology model. The vegetation variables were proportion lowland shrubs, proportion deciduous trees, and proportion coniferous trees. Because the proportions of these cover variables almost totaled 1.00, we only included up to two of the three vegetation variables in any one model. With that caveat, the geomorphology + vegetation model set was all combinations of the geomorphology and vegetation variables. In the fourth phase, we added the number of colonies within 4.9 and 11.3 km of the point to the geomorphological and vegetation variables. In this case, the two variables for source colonies were not included in the same model, since one variable is a subset of the other. With that caveat, the geomorphology + vegetation + colonizers model set was all combinations of the geomorphology, vegetation, and source colony variables.

In each phase, we ranked the models using AIC$_c$ and considered models with AIC$_c$ differences ≤ 2 (ΔAIC$_c$)to be in the competitive set of models (Burnham and Anderson 2002). The best model was considered to be the model from the competitive set with the fewest variables with 90% confidence intervals that did not include zero (*sensu* Arnold 2010). Confidence intervals were used to assess if a variable was informative or a result of overfitting (Burnham and Anderson 2002). We calculated Akaike weights (w_i) and evidence ratios (the ratio of w_1/w_i where model 1 is the model with the minimum AIC$_c$ and i indexes the rest of the models in the set) (Burnham and Anderson 2002). Evidence ratios indicate how much better the model with the smallest AIC$_c$ value fits the data compared to other models. For phases 2–4, we present the AIC$_c$ tables for the models in the competitive set plus the first model outside of the competitive set, the best models from the previous phases, and the null model. We also present tables of the coefficients, standard errors, and confidence intervals for the best models.

To examine the effect of individual predictor variables on the probability of colonization (P (colonization)), we made predictions from the best models using values within the 10th and 90th percentiles for continuous response variables and for each category for categorical variables in turn while holding other model variables constant (Shaffer and Thompson 2007). We used mean values as the constant value for continuous explanatory variables (stream gradient, valley relief, vegetation cover, and number of colonies within a specified distance from the point). For the categorical variables, we used a single category (poor drainage for drainage class, groundwater for water source, medium for stream width, alkaline for stream alkalinity, and cool for stream temperature). For each of the three best models, we calculated the percentage effect of a variable on the probability of colonization by dividing the difference between the higher and lower predicted probabilities of colonization by the lower predicted probability of colonization. This is a measure of the importance of the individual variables on the probability of colonization and allows us to determine how well the variables retain that importance across the three best models.

Model assessment (testing set)

We compared how well the best models from the three phases predicted P (colonization) using the test dataset to compare the performance of the three models (geomorphology only, geomorphology–vegetation, and geomorphology–vegetation–colonizers). We used a confusion matrix to assess the ability of the best models (derived from training data) to accurately predict colonization or absence of beaver for the test data. Probabilities greater than 0.50 were used to indicate a predicted colonization. For each model, we calculated specificity (proportion of correctly predicted absences) and sensitivity (proportion of correctly predicted colonizations). We compared these values across models and to the proportions of colonizations and absences in the test data.

All analyses were done in R version 4.0.5 (R Core Team 2021). Models were fit using generalized linear models with a binomial error structure with "glm". Colony presence was coded as 1 and absence was coded as 0. As a measure of model fit for the training data, we calculated generalized R^2 values (Nakagawa and Schielzeth 2013) with the "MuMIn" package and area under the receiver operator curve (AUC) using the "modEvA" package.

Habitat suitability

We modified the approach of Dittbrenner et al. (2018) to define beaver habitat suitability for our study area. We used the predicted P (colonization) for the entire dataset from the better of the geomorphology or geomorphology–vegetation models to determine beaver habitat suitability across the managed stream network. We divided P (colonization) into five habitat suitability categories. The categories were very poor suitability (P (colonization) ≤ 0.20), poor suitability ($0.20 < P$ (colonization) ≤ 0.40), moderate suitability ($0.40 < P$ (colonization) ≤ 0.60), good suitability ($0.60 < P$ (colonization) ≤ 0.80), and very good suitability (P (colonization) > 0.80). We calculated what fraction of the sampled landscape fell into each of the categories. As a visual display of the habitat suitability of the landscape for beaver, we mapped habitat suitability for streams on the northern part of the Eagle River-Florence District of the CNNF (Fig. 1). For mapping, we used three categories of poor, moderate, and good suitability. For the poor suitability mapping category, we combined the very poor and poor suitability classes (i.e., P (colonization) ≤ 0.40). For the good suitability mapping category, we combined the good and very good suitability classes (i.e., P (colonization) > 0.60).

Results

Colony locations and drainage classification assessment

Over the 1987–2014 period, colony removals generated 1773 colonization events (Eklund et al. 2023). Colonized streams were classified as intermittent for 38 (2.2%) of these events and were removed from analysis for a sample size of 1735 colonization events. There were 2116 absence points used for the analysis. The training set ($n = 3081$) consisted of 1372 colonization events and 1709 absence points and the test set ($n = 770$) consisted of 363 colonization events and 407 absence points.

Drainage class models

The minimum AIC_c model for beaver colonization as a function of drainage class was the two-category variable (poor and better drained soils); the three-category drainage model was in the competitive set ($\Delta AIC_c = 1.21$). In the three-category drainage model, the moderately good category was not different from the very good drainage category (coefficient = −0.73, SE = 0.194, and 90% CI: −0.491, 0.144). The seven-category drainage model was outside the competitive set ($\Delta AIC_c = 3.55$). We used the two-category drainage class model for further model development.

Geomorphology model (beaver intrinsic potential variables)

For the geomorphology model, the minimum AIC_c model was the best model and was composed of all the geomorphology variables except watershed area (Table 1). The best model (Table 2) explained 11.5% of the variability in beaver colonization events and had an AUC value of 0.676. The evidence ratio of this model compared to the constant model was over 500 000 (Table 1). The only other model in the competitive set was the minimum AIC_c model plus watershed area (Table 1). Watershed area was not informative (coefficient = 0.001, SE = 0.001, and 90% CI: −0.001, 0.003), indicating model overfit.

Colonization probability decreased as stream gradient increased and as valley relief increased (Table 2). Beavers were more apt to colonize narrow and medium streams than wide streams. Beavers also colonized cool and warm streams more than cold streams with no preference between cool and warm streams (Table 2). Beavers were more likely to colonize surface-water streams rather than groundwater streams and beavers preferentially colonized streams that were neutral rather than acid or alkaline (with no preference between acid and alkaline, Table 2). Finally, beavers colonized streams that ran through soils in the poor drainage category more often compared to soils in the better drainage category (Table 2).

Geomorphology–vegetation model

Considering both geomorphology and vegetation variables, the best model was the model with the minimum

Table 1. American beaver (*Castor canadensis*) colonization-geomorphology models in the competitive set resulting from information–theoretic model selection on geomorphology variables.

Model	N	K	AIC$_c$	ΔAIC$_c$	Akaike weight	Evidence ratio	Adj R^2	AUC
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + valley relief	3081	11	3980.7	0	0.409		0.115	0.6759
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + valley relief + watershed area	3081	12	3981.4	0.71	0.287	1.426	0.115	0.6769
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	10	3982.6	1.98	0.152	2.691	0.113	0.6750
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + watershed area	3081	11	3983.6	2.94	0.094	4.349	0.113	0.6756
Constant	3081	1	4236.2	255.58	<0.00001	3.15E + 55	0	

Table 2. Parameter estimates (coefficient) and related statistics for the best American beaver (*Castor canadensis*) habitat selection logistic regression model using geomorphology variables. Categorical variables were parameterized as (0, 1); therefore, the value of the category not listed in the table is embedded in the intercept. SE = standard error.

Variable	Coefficient	SE	P	90% Confidence interval	
Intercept	−0.531	0.195	0.006	−0.851	−0.211
Drainage class: poor	0.347	0.094	<0.001	0.193	0.501
Stream gradient	−0.216	0.08	0.007	−0.347	−0.085
Water source: surface	0.606	0.158	<0.001	0.347	0.865
Valley relief	−0.097	0.049	0.048	−0.177	−0.017
Stream width: narrow	0.229	0.101	0.024	0.063	0.395
Stream width: wide	−1.202	0.505	0.017	−2.03	−0.374
Stream alkalinity: acid	−0.384	0.357	0.283	−0.969	0.201
Stream alkalinity: neutral	0.846	0.244	<0.001	0.446	1.246
Stream temperature: cold	−0.654	0.166	<0.001	−0.926	−0.382
Stream temperature: cool	0.012	0.161	0.941	−0.252	0.276

AIC$_c$ value, which was composed of the best geomorphology model but with the valley relief and drainage class variables replaced by proportion deciduous trees and proportion lowland shrubs (Table 3). The best model (Table 4) explained 17.2% of the variability in beaver colonization events and had an AUC value of 0.715. There were three other models in the competitive set (Table 3). One model was the minimum AIC$_c$ model without stream gradient and the other two were the minimum AIC$_c$ model with drainage class or drainage class and valley relief (Table 3). However, neither drainage class (coefficient = 0.103, SE = 0.97, and 90% CI: −0.56, 0.261) nor valley relief (coefficient = −0.36, SE = 0.046, and 90% CI: −0.112, 0.039) were informative, indicating overfit models. The best geomorphology model was not competitive with the best geomorphology–vegetation model; the evidence ratio of the best geomorphology–vegetation model compared to the best geomorphology model was over 100 000 (Table 3).

Probability of colonization increased as proportion lowland shrubs increased and probability of colonization also increased as proportion deciduous trees increased but not as much compared to lowland shrubs (Table 4). Relationships with the geomorphology variables were similar to those found with the best geomorphology model. Colonization probability decreased as stream gradient increased and beavers were more likely to colonize narrow and medium streams rather than wide streams (Table 4). Beavers colonized cool and warm streams more than cold streams and beavers were more likely to colonize surface-water streams rather than groundwater streams (Table 4). Beavers preferentially colonized streams that were neutral rather than acid or alkaline (with no preference between acid and alkaline (Table 4)).

Geomorphology–vegetation–colonizer model

Considering geomorphology, vegetation, and colonizer variables, the best model was the model with the minimum AIC$_c$ value, which was composed of the best geomorphology–vegetation model with the addition of the number of colonies within 11.3 km of the stream (Table 5). The model (Table 6) explained 18.6% of the variability in beaver colonization events and had an AUC value of 0.724. There was one other model in the competitive set and it was the minimum AIC$_c$ model plus drainage class (Table 5). However,

Table 3. American beaver (*Castor canadensis*) colonization–geomorphology–vegetation models in the competitive set resulting from information–theoretic model selection on geomorphology and vegetation variables.

Model	*N*	*K*	AIC$_c$	ΔAIC$_c$	Akaike weight	Evidence ratio	Adj R^2	AUC
Deciduous trees + lowland shrubs + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	11	3833.3	0	0.190		0.172	0.7147
Deciduous trees + lowland shrubs + drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	12	3834.2	0.88	0.180	1.57	0.172	0.7150
Deciduous trees + lowland shrubs + stream alkalinity + stream temperature + stream width + water source	3081	10	3834.5	1.23	0.155	1.82	0.171	0.7136
Deciduous trees + lowland shrubs + drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + valley relief	3081	12	3834.7	1.39	0.095	2.00	0.172	0.7148
Deciduous trees + lowland shrubs + drainage class + stream alkalinity + stream temperature + stream width + water source	3081	11	3835	1.70	0.121	2.34	0.171	0.7141
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + valley width	3081	11	3980.7	147.4	1.914E − 33	9.92E + 31	0.115	0.6759
Constant	3081	1	4236.2	402.9	9.158E − 89	3.08E + 87	0	

Table 4. Parameter estimates (coefficient) and related statistics for the best American beaver (*Castor canadensis*) habitat selection logistic regression model using geomorphology and vegetation variables. Categorical variables were parameterized as (0, 1); therefore, the value of the category not listed in the table is embedded in the intercept. SE = standard error.

Variable	Coefficient	SE	*P*	90% Confidence interval	
Intercept	−1.341	0.202	<0.001	−1.672	−1.01
Stream gradient	−0.142	0.080	0.076	−0.273	−0.011
Water source: surface	0.748	0.162	<0.001	0.482	1.014
Stream width: narrow	0.112	0.104	0.280	−0.059	0.283
Stream width: wide	−1.267	0.517	0.014	−2.115	−0.419
Stream alkalinity: acid	−0.388	0.366	0.289	−0.988	0.212
Stream alkalinity: neutral	0.634	0.251	0.011	0.222	1.046
Stream temperature: cold	−0.286	0.172	0.095	−0.568	−0.004
Stream temperature: cool	0.174	0.165	0.290	−0.097	0.445
Proportion deciduous trees	0.449	0.150	0.003	0.202	0.696
Proportion lowland shrubs	1.925	0.158	<0.001	1.666	2.184

drainage class was not informative (coefficient = 0.087, SE = 0.097, and 90% CI: −0.072, 0.247), indicating an overfit. None of the models using number of colonies within 4.9 km of the stream were in the competitive set (Table 5). The best geomorphology–vegetation model was not competitive with the best geomorphology–vegetation–colonizer model; the evidence ratio of the best geomorphology–vegetation–colonizer model compared to the best geomorphology–vegetation model was about 80 000; the evidence ratio of the best geomorphology–vegetation–colonizer model compared to the best geomorphology model was even larger (Table 5).

Probability of colonization increased with more beaver colonies within 11.3 km of the stream (Table 6). Relationships with the vegetation variables were similar to those in the geomorphology–vegetation model. Colonization probability increased as proportion of lowland shrubs increased and as proportion of deciduous trees increased but not as much compared to lowland shrubs (Table 6). Relationships with the geomorphology variables were similar to those found with the geomorphology–vegetation model. Colonization probability decreased as stream gradient increased (Table 6). Beavers were more likely to colonize narrow and medium streams rather than wide streams and beavers colonized cool and warm streams more than cold streams (Table 6). Beavers were more likely to colonize surface-water streams rather than groundwater streams, and streams that were neutral rather than acid or alkaline (Table 6).

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Table 5. American beaver (*Castor canadensis*) colonization–geomorphology–vegetation–colonizer variable models in the competitive set resulting from information–theoretic model selection on geomorphology, vegetation, and source colony variables.

Model	*N*	*K*	AIC_c	ΔAIC_c	Akaike weight	Evidence ratio	Adj R^2	AUC
Colonies within 11.3 km + deciduous trees + lowland shrubs + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	12	3796.9	0	0.275		0.186	0.724
Colonies within 11.3 km + deciduous trees + lowland shrubs + drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	13	3798.1	1.21	0.150	1.83	0.187	0.724
Colonies within 11.3 km + deciduous trees + lowland shrubs + stream alkalinity + stream temperature + stream width + water source	3081	11	3798.4	1.51	0.129	2.13	0.185	0.723
Colonies within 11.3 km + deciduous trees + lowland shrubs + drainage class + stream alkalinity + stream temperature + stream width + water source	3081	12	3799.2	2.32	0.086	3.19	0.185	0.723
Deciduous trees + lowland shrubs + stream alkalinity + stream gradient + stream temperature + stream width + water source	3081	11	3833.3	36.4	<0.0001	8.02E + 07	0.172	0.715
Drainage class + stream alkalinity + stream gradient + stream temperature + stream width + water source + valley width	3081	11	3980.7	183.8	<0.0001	8.16E + 39	0.115	0.676
Constant	3081	1	4236.2	439.3	<0.0001	2.47E + 95	0	

Table 6. Parameter estimates (coefficient) and related statistics for the best American beaver (*Castor canadensis*) habitat selection logistic regression model using geomorphology, vegetation, and source colony variables. Categorical variables were parameterized as (0, 1); therefore, the value of the category not listed in the table is embedded in the intercept. SE = standard error.

Variable	Coefficient	SE	*P*	90% Confidence interval	
Intercept	−1.523	0.205	<0.001	−1.859	−1.187
Stream gradient	−0.148	0.080	0.064	−0.279	−0.017
Water source: surface	0.683	0.161	<0.001	0.419	0.947
Stream width: narrow	0.086	0.105	0.414	−0.086	0.258
Stream width: wide	−1.226	0.518	0.018	−2.076	−0.376
Stream alkalinity: acid	−0.339	0.364	0.351	−0.936	0.258
Stream alkalinity: neutral	0.690	0.249	0.006	0.282	1.098
Stream temperature: cold	−0.280	0.171	0.102	−0.560	0.000
Stream temperature: cool	0.118	0.165	0.474	−0.153	0.389
Proportion deciduous trees	0.413	0.152	0.006	0.164	0.662
Proportion lowland shrubs	1.913	0.159	<0.001	1.652	2.174
Colonies within 11.3 km	0.021	0.003	<0.001	0.016	0.026

Individual variable effects on *P* (colonization)

Overall, the most important geomorphology variables predicting the probability of colonization were stream width and stream alkalinity (Table 7). Stream width retained most of its effect across all three models, but stream alkalinity lost a third of its effect once site vegetation was known (Table 7). In fact, most of the geomorphology variables lost impact once vegetation variables were added to the model (Table 7). Interestingly, while adding vegetation information had substantial effects on the importance of geomorphological variables, number of source colonies did not have much impact on either the geomorphology or vegetation variables even though number of source colonies had the second strongest effect on the probability of colonization in its model (Table 7).

Accuracy of predicted colonization probabilities

Using the best geomorphology model to predict colonization in the test data resulted in an overall % correctness of 63.1%. Specificity was 74.9% for absences correctly predicted and sensitivity was 49.9% for colonizations correctly predicted. This model predicted absences better than colonizations compared to the proportions in the test data (52.9% absences and 47.1% colonizations).

Using the best geomorphology–vegetation model to predict colonization in the test data resulted in an overall per-

Table 7. Effects and relative effect sizes of model variables on probability of colonization by American beaver (*Castor canadensis*) (*P* (colony)) for the geomorphology model (Geomorph), geomorphology and vegetation model (Geomorph + veg), and geomorphology, vegetation, and colonizer model (Geo + veg + colonizer).

		Geomorph		Geomorph + veg		Geo + veg + colonizer	
Variable	Value	*P* (colony)	Effect	*P* (colony)	Effect	*P* (colony)	Effect
Stream gradient	0.10%	0.429	75%	0.368	47%	0.381	48%
	4.00%	0.245		0.251		0.257	
Stream width	Narrow	0.47	169%	0.372	174%	0.381	157%
	Medium	0.413	136%	0.372	174%	0.381	157%
	Wide	0.175		0.136		0.148	
Stream temperature	Cool/warm	0.413	54%	0.379	28%	0.385	25%
	Cold	0.268		0.296		0.308	
Stream source	Surface	0.564	37%	0.542	51%	0.539	45%
	Ground	0.413		0.359		0.371	
Stream alkalinity	Neutral	0.621	92%	0.513	62%	0.54	62%
	Other	0.324		0.317		0.333	
Soil drainage	Poor	0.413	24%		0%		0%
	Other	0.332					
Valley relief	0.07	0.431	12%		0%		0%
	1.99	0.386					
Proportion deciduous trees				0.405	18%	0.414	16%
				0.342		0.356	
Proportion lowland shrubs				0.575	92%	0.587	89%
				0.299		0.311	
Number of source colonies						0.621	92%
						0.323	

centage of correct predictions of 64.3%. Specificity was 76.7% for absences correctly predicted and sensitivity was 50.4% for colonizations correctly predicted. While slightly improving on predicting colonization events, the geomorphology–vegetation model was best at predicting absences, similar to the geomorphology model.

Using the best geomorphology–vegetation–colonizer model to predict colonization in the test data resulted in an overall percentage of correct predictions of 65.5%. Specificity was 73% for absences correctly predicted and sensitivity was 57% for colonizations correctly predicted. This model was slightly inferior for predicting absences but predicted actual colonizations better compared to the best geomorphology and geomorphology–vegetation models.

Across the study landscape, the geomorphology–vegetation model rated 6.4% of sampled sites as very low and 38.3% as low suitability for beaver. Conversely, >50% of the sites on managed streams were predicted to have moderate (31.9%) or good (21.5%) suitability for beavers. Habitat of very good quality suitability made up the rest (1.9%). Habitat suitability for beavers was a mosaic along the stream system (Fig. 2).

Discussion

We used a large-scale, long-term beaver removal program conducted on streams within the CNNF to model and predict initial colonization events of beaver. Annual removal of beaver allowed for repeated colonization events on managed streams with limited manipulation of habitat by beaver; thus, results indicate which vegetation and stream characteristics were important to beaver prior to any ecosystem engineering.

The best geomorphology model used six of the seven candidate variables, discarding only watershed size. There was substantial overlap in variables used with the BIP model of Dittbrenner et al. (2018). Variables in common were stream gradient, stream width, and valley relief (valley width in Dittbrenner et al. 2018); we found additional relationships with stream temperature, stream water source, stream chemistry, and soil drainage. Dittbrenner et al. (2018) obtained soil drainage data but did not include that in their model for reasons that were not described. Overall, the geomorphology model for the CNNF is much less effective at predicting favorable beaver locations than Dittbrenner et al.'s (2018) model was for predicting use of sites in the Snohomish River basin (state of Washington). This probably reflects substantive differences in the two study sites, as the Snohomish River basin provides a much starker set of choices to beavers. Dittbrenner et al. (2018) found that 60% of Snohomish River stream segments had no potential for beaver and another 8% had only low suitability, whereas 23% were highly suitable and 10% were moderately suitable. In contrast, our geomorphology model predicted the CNNF landscape to be <5% in very poor

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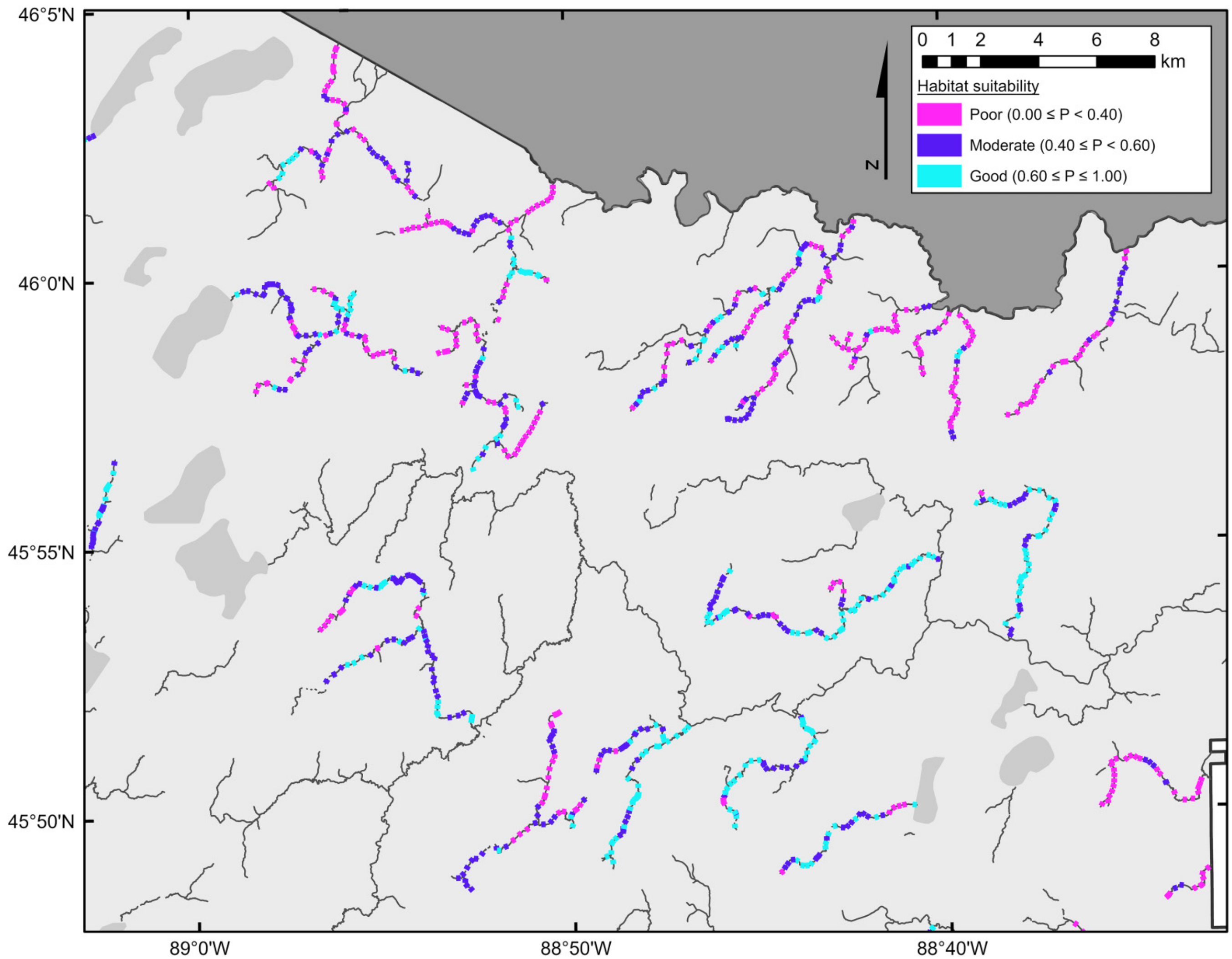
Fig. 2. Predicted habitat suitability for American beaver (*Castor canadensis*) on the northern part of the Eagle River-Florence District of the Chequamegon-Nicolet National Forest. Suitability is based on the predicted probability of colonization (*P*) using the best geomorphology and vegetation model. Map projection is NAD 1983 HARN Wisconsin TM (meters). The map has three components: state boundaries (National Atlas of the United States 2013*b*), inland waters (National Atlas of the United States 2013*a*), and Wisconsin stream network (Wisconsin Department of Natural Resources 2017*b*).



suitability and only 1% in very high suitability. The bulk of the CNNF landscape is predicted to be of moderate/high suitability (57%) or low suitability (38%) from a purely geomorphological perspective.

Considering geomorphology variables more broadly, we found no explanatory power from watershed size. This differs from the models reviewed by Touihri et al. (2018), in which watershed size was important in three of the four models that included it. This may be related to the general abundance of water in this landscape and the relatively flat topography, as it does not require a particularly large watershed to capture enough water for an effective beaver pond. Our results also provide additional insight into the effect of stream width. While the models reviewed by Touihri et al. (2018) found either a positive or negative effect, our model indicated a potential nonlinear effect with a flat effect (transitioning from narrow to medium width streams) and then a negative effect (transitioning from medium to wide streams). Distinguishing between nonlinearity, stream width definitions, analysis approaches, and actual differences in relationships would be an interesting question to resolve and would most easily be done by integrating the datasets underlying the various models.

The best geomorphology–vegetation model explained 50% more of the variability than the geomorphology model. It retained the stream gradient, stream width, stream temperature, stream water source, and stream chemistry variables. While it remained in the model, stream gradient lost much of its utility. Valley relief and drainage class variables were replaced by proportion deciduous trees and proportion lowland shrubs. Therefore, the vegetation variables provided the model with information on some aspects of geomorphology, while revealing the importance of dam-building materials and food availability to explain habitat selection by beaver. Of the 11 models reviewed by Touihri et al. (2018) that considered deciduous cover, five found a positive relationship; the other six found no relationship. Of the nine models reviewed by Touihri et al. (2018) that considered shrub cover, one found a positive relationship, six found no relationship, and two found a negative relationship. Our study not only found a positive relationship for shrub cover, but it was a much stronger relationship than for deciduous cover. On the CNNF, the riparian shrub cover is primarily alder (*Alnus* spp.) and willow (*Salix* spp.), which are favored by beaver for construction and consumption, respectively (e.g., Gallant et al. 2004).

Density of potential colonizers has not been included in the previous beaver habitat selection models. In our study, beaver movements that ended in colonization events on targeted streams most likely represented dispersal events because removed beavers were predominantly male and 2 years of age (Animal and Plant Health Inspection Service 2012), which corresponds to the age of natal dispersing beaver (Svendsen 1980). Also, our model indicates that colonizers likely were coming from farther away rather than nearby. This may reflect the special conditions of our study area, characterized by beaver management practices that ensured the annual availability of a substantial amount of uncolonized but suitable space, allowing more choices for a larger number of beavers as they moved across the landscape. Beaver colonization of remote areas (Jung et al. 2016) indicates that beavers can move long distances before selecting a place to settle.

Overall, despite having identified seven variables that provided a useful insight into the probability of a site being colonized by beaver, even our best logistic regression model was only able to correctly predict presence/absence status in 65% of the test cases. There was, however, marked asymmetry in the model's predictive capability. The model took advantage of the fact that absence points were defined as sites that had not been colonized in over 25 years and was able to correctly predict 73% of the test set absence points. While it would have been rewarding to predict absence better, models that predict initial colonization by beavers are always going to have absence errors because the beavers make selection mistakes. For example, we know from this dataset that 2% of colonization attempts were on intermittent streams, which cannot sustain the new colony. Previous work has also shown that beavers re-disperse relatively often. For example, Sun et al. (2000) found that 36% of beavers in a New York state park moved after their first dispersal action.

The observed 57% success in predicting presence is relatively low compared to the success rate of beaver habitat selection models for the western United States, which is often greater than 80%. While this can reflect a number of factors, our conjecture is that two key factors account for the low performance. First, this landscape is broadly attractive to beavers. As noted in the discussion of the geomorphology model, the mountainous western landscape in Washington state studied by Dittbrenner et al. (2018) is either clearly useless (>60% of the landscape) or of low suitability (8% of the landscape) for beavers. Across our low relief upper Midwest study landscape, the geomorphology–vegetation model rates most of the available sites on managed streams be moderate or better quality habitat for beavers. Second, the population of unmanaged beavers is simply not large enough for dispersers to colonize all available suitable sites. As Ribic et al. (2017) showed, the unmanaged population had declined over the course of 25 years of management. Consequently, in any given year, a substantial fraction of suitable sites could not be selected simply due to a lack of beavers to choose those sites, creating a substantial presence prediction error. This was particularly evident on the Nicolet side of the CNNF, which experienced the greater decline (Ribic et al. 2017). The probability of a beaver colonizing a Nicolet site in year i that had also been used in year $i-1$ or year $i-2$ was 0.32 over the first five years of observation—but had dropped to 0.13 by the last five years of observation.

Prediction weaknesses notwithstanding, these models provide a better foundation for understanding beaver habitat suitability in the upper Midwest. Because our results show the landscape to be mostly suitable for beavers (i.e., flatter, rich in water, high availability of food and dam building materials and hence low predictability), some level of a targeted beaver control program remains warranted as maintaining cold-water streams remains a management priority for CNNF (see Johnson-Bice et al. 2018). However, our results also suggest that past forest habitat management activities on adjacent tributaries or feeder areas have created highly desirable conditions for colonization by beavers (high shrub cover associated with cool/warm waters and a low stream gradient). Focusing habitat management in these areas instead of only the main stem of cold-water streams, as is currently done, may be an additional strategy to lower colonization events in key areas. For example, would converting shrub areas to a forested system such as tamarack, or other tree species that is associated with the existing water regime, have the effect of naturally reducing shrub cover, thereby making an area less suitable for beaver colonization? By removing this preferred habitat near cold-water streams, it may also improve the effectiveness of beaver removal and reduce costs over time as the new forest habitat establishes and converts to a type of less beaver-friendly forested system. Such an approach also promotes a multiple-use framework focused on balancing public and wildlife needs by targeting beaver management on some areas instead of all areas. Determining the effectiveness of integrating a landscape-scale design in forest habitat management activities into current large-scale beaver control programs aimed at lowering beaver numbers in targeted systems warrants further exploration.

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Data availability

Data generated or analyzed during this study are available in the Forest Service Research Data Archive repository, https://doi.org/10.2737/RDS-2023-0019.

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Competing interests

The authors declare there are no competing interests.

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