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Habitat relationships and gene flow of Martes americana in northern Idaho

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HABITAT RELATIONSHIPS AND GENE FLOW OF *MARTES AMERICANA* IN NORTHERN IDAHO

By

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Accepted in Partial Completion
of the Requirements for the Degree of
Master of Science

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MASTER'S THESIS

HABITAT RELATIONSHIPS AND GENE FLOW OF <u>MARTES AMERICANA</u> IN NORTHERN IDAHO

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
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February 2008

ABSTRACT

Forest fragmentation can have a dramatic effect on landscape connectivity and dispersal of animals, potentially reducing gene flow within and among populations. American marten populations (*Martes americana*) are sensitive to forest fragmentation and the spatial configuration of patches of remnant mature forest has an important impact on habitat quality. This study represents an extensive multiple scale habitat relationships analysis conducted for American marten. In conjunction with Idaho Department of Fish and Game (IDFG) and the U.S. Forest Service, genetic data on marten populations across the Idaho Panhandle National Forest was used to build habitat relationships models. Over 3 years of winter fieldwork during 2004, 2005, and 2006, I detected martens at 569 individual hair snare stations distributed across a 3,000 square kilometer study area covering the Selkirk, Purcell, and Cabinet Mountain ranges.

I investigated habitat relationships of this population of *Martes americana* in the Idaho Panhandle National Forest (IPNF) at three spatial scales: Plot, Home Range, and Multiple-Scale. I used bivariate scaling to measure each environmental variable across a broad range of radii ranging from 90m-1080m around each sample station. I used an information-theoretic approach to rank 45 *a priori* candidate models that described hypothesized habitat relationships at each spatial scale. At the plot scale, marten presence was positively predicted by the Percentage of Landscape (PLand) comprised of large sawtimber, and negatively predicted by PLand of seedling/sapling timber type. At the home range scale, the probability of detecting a marten decreased with increasing amounts of fragmentation and highly contrasted edges between patches of large sawtimber and patches of seedling/sapling and non-stocked patches.

In the multiple-scale analysis, I used a variable screening step to find variables that were universal and consistent throughout all models in order to build candidate models. PLand comprised of large homogeneous patches of large sawtimber was a positive predictor of marten presence, while highly contrasted edges and fragmentation were strong negative predictors of marten presence. The scale at which martens selected habitats varied greatly across variables. Martens actively selected for high quality habitat at the fine scale (plot level) and strongly avoided areas comprised of seedling/sapling and non-stocked timber areas. Martens negatively responded to high contrast edges and strongly avoided them. Juxtaposition and configuration of patches of large sawtimber was important to marten habitat selection. This study demonstrates the importance of investigating marten habitat at multiple spatial scales and provides insights to linkages among scales and how martens respond to forest fragmentation.

Genetic information was used to model genetic relationships of this marten population with respect to environmental and spatial variables within my study landscape. Over three field seasons 70 individual marten were detected across the study area. The genetic similarities were based on the pair-wise percentage dissimilarity among all individuals based on 7 microsatellite loci. I compared their genetic similarities with several landscape resistance hypotheses. The landscape resistance hypotheses describe a range of potential relationships between movement cost and landcover, elevation, roads, Euclidean distance and valleys between mountain ranges as barriers. The degree of support for each model was tested with causal modeling on resemblance matrices using partial Mantel tests.

Hypotheses of Isolation by Distance and Isolation by Barrier were not supported, and Isolation by Landscape Resistance proved to be the best model describing genetic patterns of *Martes americana* in the IPNF. Elevation 1600m with a standard deviation of 600m was the most highly supported landscape resistance model correlated to genetic structure of marten in this landscape. Correlating genetic similarity of individuals across large landscapes with hypothetical movement cost models can give reliable inferences about population connectivity. By linking cost modeling to the actual patterns of genetic similarity among individuals it is possible to obtain rigorous, empirical models describing the relationship between landscape structure and gene flow, and to produce species-specific maps of landscape connectivity, and can provide managers with critical information to better administer our forests for meso-carnivores and other species of concern.

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This work was part of a cooperative research project on the American marten (*Martes americana*) and fisher (*Martes pennanti*) in conjunction with Idaho Department of Fish and Game, the U.S. Forest Service, and Western Washington University. This work was possible thanks to the hard work and encouragement of Jim Hayden of the Idaho Department of Fish and Game who gave me great support. Funding for this project was provided and by Idaho Department of Fish and Game, the U.S. Forest Service Rocky Mountain Research Station, and grants from Huxley College of the Environment and Western Washington University Bureau for Faculty Research. I would like to thank my committee: David O. Wallin, Leo R. Bodensteiner, and Michael K. Schwartz for their guidance and support. Thank you for all the hard work contributed by the many technicians and volunteers who helped collect this data. Thank you to the Wildlife Genetics Lab in the U.S. Forest Service Rocky Mountain Research Station for aid in genetic analysis. Mostly, I would like to thank my family for their ongoing encouragement, support and advice.

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CHAPTER 1:

Multiple-Scale Habitat Relationships of American marten (*Martes americana)* in northern Idaho

INTRODUCTION

The information theoretic approach has become the dominant paradigm for use in wildlife habitat selection studies (Burnham and Anderson 2002; Johnson and Omland 2004). Although the advantages of this approach have been extensively reviewed (but see Guthery et al. 2005 and Stephens et al. 2005), very little attention has been given to scaling issues when selecting variables for inclusion in candidate models. For most species, a priori information is available to guide decisions regarding appropriate variables for inclusion in candidate models. However, the effect of a given variable on habitat selection may manifest itself at spatial scales ranging from a few meters to kilometers (e.g. Thompson and McGarigal 2002). A priori, it is problematic to determine which scale is most appropriate (Levin 1992). Most habitat selection studies fail to address this issue and simply evaluate alternative models that are based on predictor variables from a single, arbitrarily selected scale. In this study, I introduce a multiple-scale approach to developing habitat selection studies. I illustrate this approach by developing and evaluating multiple-scale habitat selection models for the American marten (*Martes americana*) in northern Idaho.

American marten in the Rocky Mountains have been shown to be tightly associated with late-successional coniferous forests (Buskirk and Powell 1994; Campbell 1979; Soutiere 1979; Stevenson and Major 1982; and Wilbert 1992). Forest carnivores such as marten require relatively large areas of late-successional forest within their home ranges and these late-successional forests are predominantly found on public lands. As a result of the conversion of extensive tracts of late seral forest to fragmented mosaics of mixed seral stages following timber harvest, the geographic ranges of many forest carnivore species have been dramatically reduced. Currently, at least 65% of the geographic range of American marten is found on public lands (Buskirk and Ruggiero 1994).

Management policies on public forestlands are among the most contentious and politically charged issues in the region. Much of the controversy involves balancing economic and social issues such as recreation and timber production, with ecological issues such as wildlife preservation. Late-successional forests are home to many species of plants, birds, and mammals that rely on this floristic stage as their primary habitat for foraging and reproduction. Late-successional forests are also in prime stage for timber harvesting activities, which provide economic and social gains to many people. In 1976, the U.S. Congress passed the National Forest Management Act, which mandated maintaining biological diversity on lands within the National Forest System. The implementation and interpretation of the requirements of this act continue to drive many legal challenges to forest management policies and practices on our national forests.

Objectives

This study is intended to characterize the habitat relationships of American marten populations in the Idaho Panhandle National Forest (IPNF) in northern Idaho and expand the scientific knowledge of this species in the Northern Rocky Mountains. This knowledge is intended to help guide future management of marten populations in this study area, as well as other species with similar habitat requirements within the region. I will accomplish this by using multi-model inference in a logistic regression framework to predict suitable marten winter habitat at the landscape-level based on multiple-scale environmental data, and then develop multiple scale habitat relationship models for American marten to predict occurrence based on habitat and disturbance history. Working jointly with the Idaho Department of Fish and Game (IDFG) and the U.S. Forest Service (USFS) the goal of this study is to evaluate important components of marten habitat selection at a variety of spatial scales as well as determine the genetic relationships of all individual marten detected across the study landscape.

For any given variable, there is no a priori way to know the spatial extent surrounding the sample point at which the variable is most strongly related to marten presence. Therefore, it is best to measure each environmental variable across a broad range of radii surrounding each sampled plot to determine the scale(s) at which each predictor variable is most related to the response (Cushman et al. 2007). Bivariate scaling (Grand et al. 2004; Thompson and McGarigal 2002) has been shown to be a highly effective method for identifying the appropriate scale in species-environment relationship modeling. Characterizing the landscape surrounding each point at multiple scales facilitates the selection of the appropriate scale(s) at which each aspect of landscape composition was most significant for my focal species. The patterns of the response variable (predicted probability of marten presence) are associated with multiple environmental variables, and each variable is likely to most strongly influence habitat selection at a different spatial scale. Previous habitat relationship studies on *Martes americana* have not considered these scaling issues. My objective is to identify the variables that most strongly influence habitat selection for *Martes americana* in northern Idaho and the scale at which each of these variables is most important.

Marten Ecology

The American marten (*Martes americana*) is a forest carnivore that occupies a narrow range of habitat types in coniferous forests. It is one of seven species in the genus *Martes*, in the family Mustelidae, and order Carnivora (Corbet and Hill 1986). American marten have been historically trapped for their fur over much of their range. Currently, American marten are not considered threatened or endangered in the state of Idaho and are managed as a furbearer species by the state. The USFS Region 1 has designated American marten as a management indicator species in the Idaho Panhandle National Forest in northern Idaho. According to NatureServe, the Global Conservation Status Rank of *Martes americana* is G5; secure, common, widespread and abundant. Within the state of Idaho, the NatureServe ranking is S5, indicating the population is secure, common, widespread, and abundant (Nature Serve 2008).

American marten are broadly distributed and its range extends from spruce-fir forests in northern New Mexico to arctic Alaska and Canadian forest limits, as well as from the Californian southern Sierra Nevadas to Newfoundland Island (Hall 1981). In the western contiguous United States its distribution is limited to forests and mountain ranges that provide preferred habitat containing mature forests (Buskirk and Ruggiero 1994). American marten associate with late-successional stands of mesic conifers that provide extensive complex physical structure at or near the ground (Buskirk and Powell 1994). American marten have been documented inhabiting talus fields above treeline

(Streetere and Braun 1968), however they are rarely found below the lower elevational limit of trees or in non-forested areas. American martens are mid-size carnivorous animals with a total length between 500-680 mm and weighs between 500-1400 grams as an adult, with males being 20-40% larger than females. Diet of the American marten includes insects, small mammals, berries, eggs, and nestlings (Koehler and Hornocker 1977; Simon 1980). American martens hunt for small mammals on the ground or on the surface of the snow. Prey that live beneath the snow are caught by entering the subnivean space created by coarse woody debris and other woody structures (Corn and Raphael 1992; Koehler et al. 1975). Avoidance of predators such as coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and Great-horned owls (*Bubo virginianus*) is thought to be a strong driver of habitat selection, and is reflected in their strong avoidance of open areas (Hawley and Newby 1957). American martens avoid open areas lacking overhead cover and coarse woody debris that provide protection from predators (Drew 1995).

The mechanisms by which martens are impacted by timber harvesting are when overhead cover and large diameter coarse woody debris are removed, as well as when mesic sites are converted to more xeric sites with associated changes in prey communities, as in the case of clear-cutting (Campbell 1979). Structural features that develop with succession, such as overhead cover, large diameter coarse woody debris structure, and horizontal heterogeneity of vegetation are all extremely important to marten habitat selection. Studies by Fager (1991), Koehler and Hornocker (1977), Soutiere (1979), Simon (1980), Slauson (2003) and Spencer et al. (1983) have all reported complete or partial avoidance of non-forested habitats. Landscape patterns have been shown to be important to marten habitat selection. Collectively, these previous studies suggest that martens build home ranges from landscapes rather than stands, and overall structural complexity and juxtaposition of stands within the landscape is important.

Habitat Associations

Landscapes are often described as spatially heterogeneous areas composed of a mosaic of habitat patches (Turner 1989). An individual patch differs from its surroundings in both composition and structure, and the mosaic of habitat patches is considered dynamic in both space and time (Wiens 1976). The composition, structure, number, area, distribution, size, and configuration of these patches defines the structure of the landscape. Landscapes and their structural elements are perceived uniquely by different species (Kotliar and Wiens 1990), and the quality of elements within the landscape determines how an animal will move and use the resources within that landscape. The scale in which humans perceive habitat is likely much different than that experienced by the animal. The way in which each animal interacts with the landscape is influenced by the spatial and temporal scales over which it subsists and the configuration of the landscape itself (Turner and Gardner 1991). For martens, capture rates have been shown to decrease with increasing proximity of open areas as well as increasing extent of high contrast edges (Hargis et al. 1999). Clearly, both structural elements as well as landscape patterns are important for American marten.

The American marten is considered one of the most habitat-specific mammals in North America (Buskirk and Ruggiero 1994; Harris 1994). Several studies have found that there are seasonal differences in the ages of stands used by martens, with selection for older forests during the winter (Buskirk and Ruggiero 1994). American martens are highly mobile animals and have home ranges that are 3-4 times larger than predicted for a 1 kg terrestrial mammalian carnivore (Buskirk and Ruggiero 1994). Home range size has been shown to vary depending on prey abundance and habitat type (Soutiere 1979; Thompson and Colgan 1987). Home ranges for American marten have been shown to vary significantly among sites for males, but not for females. The largest documented home range was found to be 15.7 km² in Minnesota (Mech and Rogers 1977), and was 25 times the size of the smallest home range (male mean = 0.8 km²) reported by Burnett (1981) in Montana. Male home range sizes were 1.9 times those of females. Home ranges in landscapes with clearcuts can be from 1.5 to 3.1 times greater than those from landscapes without clearcuts (Thompson and Colgan 1987). Katnik (1992) found that in an industrial forest site, martens occupied home ranges that included more mature forest and less clearcut and regenerating forest relative to their availability. In an adjacent forest reserve, where clearcuts and regenerating forest were not present, martens did not exhibit selection at the home-range scale (Chapin et al. 1998). Martens appear to consider habitat heterogeneity, interspersion, and juxtaposition when establishing a home range. In my study area in the Idaho Panhandle National Forest, marten home range is thought to be between 1.6 and 1.9 km² (Burnett 1981; Tomson 1999), and is considerably smaller than other documented home ranges.

Particular species select habitat across a hierarchy of scales. The effect of scale can be studied by examining habitat relationships across a variety of spatial scales. Individual animals respond to their environment over several spatial scales, with the smallest scale corresponding at the grain of the animal, and the largest scale being as large as its home range (Kotliar and Wiens 1990). An animal's life history needs, including foraging, resting, and searching for mates motivate habitat selection at each of these scales (Bissonette et al. 1997). Habitat selection studies should therefore examine which habitat characteristics are most important to consider and at what spatial scale they should be measured (Johnson 1980). Multiple-scale investigations are more robust over single-scale investigations because studies conducted over several spatial scales facilitate a greater understanding of how animals assimilate information and make decisions that influence habitat selection (Ritchie 1997; Slauson 2003). In this study, I examined marten occurrence with respect to environmental features across multiple scales ranging from the plot scale (90 m) to the landscape scale (1080 m) in 90 m increments around the point of detection.

Habitat use by American marten is dependent on a variety of spatial scales. At the finest scale, martens select habitat features that provide foraging, resting, and denning sites. Martens exhibit seasonal variation in the types of prey and forage items utilized (Martin 1994; Strickland and Douglas 1987). Mammal species include voles (*Clethrionomys, Microtus*), red squirrels (*Tamiascurius ruficanus*.), ground squirrels (*Spermophilus*), and chipmunks (*Tamias*), and are important components of their diet in the western United States (Martin 1994). These species are most important during the winter months when prey options are most limited (Buskirk and Ruggiero 1994). This seasonal variation in forage preference can result in seasonal variation in the habitat selection at a fine scale. However, it should be noted that marten do not undergo seasonal shifts in the size of their home ranges. In the western U.S., prey species such as red-backed voles (*Clethrionomys gapperi*) and red squirrels (*Tamaisciurus ruficanus*) are closely associated with components of late successional forests. Both of these species are more abundant in mature coniferous forests than in young open canopy areas.

Within the stand and home range scales, martens select structures for resting and denning that will provide protection from both the thermal environment as well as predators (Buskirk and Powell 1994; Taylor 1993). Variation in use of these structures changes seasonally, with above-ground structures used more during summer and fall and subnivien structures used more during winter (Chapin et al. 1998; Gilbert et al. 1997; Raphael and Jones 1997; Wilbert 1992). Resting and denning sites are most commonly located in woody structures (live trees, snags, logs) that tend to be in the largest available size classes and are used disproportionate to their availability (Gilbert et al. 1997; Raphael and Jones 1997; Ruggiero and Pearson 1998; Wilbert 1992).

Loss and fragmentation of mature forest and the resulting changes in landscape pattern constrain animal movement (Bissonette et al.1989; Chapin 1995; Hargis 1996) and demography (Fredrickson 1990; Hargis 1996). Martens respond negatively to low levels of fragmentation with capture rates decreasing with increased rates of fragmentation, and were absent in landscapes with >25% non-forest cover (Hargis et al. 1999). Studies conducted in Maine, Utah, and Quebec found that martens appear to avoid landscapes with more than 25-30% of mature forest removed (Bissonette et al. 1997; Potvin et al. 1999). Landscape characteristics, such as distance between small and large patches have been shown to influence the use of patches by martens (Chapin et al. 1998). Phillips (1994) demonstrated that martens used only 33% of the available landscape in the industrial forest site, while they occupied >80% of the landscape in a nearby forest preserve.

Study Area

The study area encompasses the Bonners Ferry and Priest River Ranger Districts on the Idaho Panhandle National Forest (IPNF) (Figure 1). The area primarily consists of the Selkirk, Purcell, and Cabinet Mountains encompassing a 3,000 square kilometer landscape. The topography is mountainous, with steep ridges, narrow valleys and many cliffs and cirques at the highest elevations. Elevation ranged from approximately 700 m to 2400 m above sea level. The Kootenai River trench runs down the middle of the study area, separating the Selkirk Mountains on the west from the Purcell and Cabinet Mountains on the east, with a five to seven mile wide unforested, agricultural valley and a broad, deep river between. The climate is characterized by cold, wet winters and mild summers. The area is heavily forested, with *Abies lasiocarpa* and *Picea engelmannii* codominant above 1300 meters, and a diverse mixed forest of *Pseudotsuga menziesii*, *Pinus contorta*, *Pinus ponderosa*, *Pinus monticola, Abies grandis*, *Tsuga heterophylla, Thuja plicata, Larix occidentalis, Betula papyrifera, Populus tremuloides, Populus trichocarpa* dominating below 1300 meters. The climate varies with respect to the elevational and topographic gradients. Temperatures range from an average high of 28.3 °C in July to an average low of 0 °C in January. Precipitation ranges from a mean of more than 1,778 mm in the highest peaks to less than 762.0 mm within the rain shadow of the Selkirk Mountains.

METHODS

Survey Methods

Hair snares were set along transects across the IPNF during the winter months of January, February, and March of 2004, 2005 and 2006. Transects consisted of a range of elevational and topographic gradients. Each snare consisted of a 1m X 1m corrugated plastic sheet folded into a triangular tunnel with metal mesh wire placed on the back end of the snare, creating a one-way opening. Snares were baited with deer meat and beaver castor placed at the back of the trap. A commercial call lure called gusto (Minnesota Trapline Products) was also dabbed onto a sponge and hung above the trap. Each trap was lined with 5 copper wire 30-caliber gunbrushes to non-invasively obtain hair samples from animals visiting the snare. Snares were set for 2 weeks after which each station was revisited to collect hair samples and re-baited for another 2-week cycle. During the check, hair was collected from the gunbrushes using tweezers and put into plastic tubes filled with dessicant and individually labeled. Each gunbrush is considered a single sample.

Genetic Methods

Hair samples were sent to the Rocky Mountain Research Station (RMRS) Wildlife Genetics Lab in Missoula, MT. Hair samples taken from each gunbrush were genetically analyzed at both the species and individual level. Once hair samples were obtained, samples were processed to extract mitochondrial Deoxyribonucleic Acid (DNA) and separate it from other cellular material. A primer is added and Polymerase

Chain Reaction (PCR) is performed to amplify and replicate the DNA strand. Bands are then separated by size via agarose gel electrophoresis and compared with a DNA ladder, which contains DNA fragments of known size, and ran on the gel alongside the PCR products. Species identification was determined using diagnostic restriction enzyme patterns followed by amplification of a region of cytochrome b on mitochondrial DNA. Following DNA amplification, PCR products were digested in three restriction reactions with *Hinf*I, *Hae*III, and *Mbo*I (Riddle et al. 2003). This method allows the discrimination of mustelid species from all other species. Martens are recognized from the location of the band on the PCR, and this method was also used to identify other species within the family Mustelidae, such as fisher (*Martes pennanti*) and wolverine (*Gulo gulo*).

Habitat Modeling

I developed and analyzed a series of models to determine the relative importance of various factors on marten habitat selection. A priori, I hypothesized that variables including elevation, moisture index, road density, vegetation type, and seral stage would have a strong influence on marten occurrence within the landscape. Elevation and moisture index were extracted from a Digital Elevation Model (DEM) of the study area (USGS 2000) and developed into individual raster grids using ArcGIS (ESRI 2003). Moisture index, also known as Topographic Wetness Index (TWI), was developed by Beven and Kirkby (1979). It is defined as ln(a/slope) where a is the local upslope area draining through a certain point per unit contour length. Both base maps were re-sampled to 30 m pixel size. Focal Mean statistics were calculated across 12 scales ranging from 90 m (plot level) to 1080 m (landscape level) in 90 m intervals. A scaling endpoint of 1080 m was chosen because it encompassed the upper end of the largest possible marten home range that could exist in this study area (Tomson 1999).

A kernel density function was calculated for road density within my study area. There were 2 classes of roads: All Roads and Open/Gated roads (Sloan et al. pers com.). The All Roads layer included paved and dirt roads within the study area that are both maintained and unmaintained. This designation includes logging roads that are grown over, and decommissioned roads that are currently not drivable but may still provide movement corridors for animals. Open/Gated Roads are both paved and dirt roads that are maintained by the USFS and the county, and are passable by vehicles. This roads layer was re-sampled to 30 m pixel size. Density of roads is calculated with a kernel method using the Point Density function in ArcGIS (ESRI 2003). This calculates the density of roads within a kernel (weighted function) of a specified radius. Road effects are then based on this kernel, which specifies a distance function. In this case, specified distances (scaling) were 180 m-1980 m in 180 m increments around each cell.

This study area contained lands managed by US Forest Service, private lands, as well as Idaho State lands. I compiled GIS layers of seral stage and vegetation type, which were obtained from the USFS Idaho Panhandle National Forest vegetation survey as well as the Idaho Department of Lands (IDL). I created a layer that was a merged map combining the current USFS IPNF Stands map (Art Zack pers. comm.) and the IDL Timber Type map depicting Diameter at Breast Height (DBH) size classes within timber stands contained in my study area (IDL 2006). DBH size classes and their descriptions are found in Table 1. Base maps were re-sampled to 30 m pixel size.

I conducted a moving window analysis with FRAGSTATS (McGarigal et al. 2002) to calculate a selection of metrics for focal window sizes from 90 m-1080 m in 90 m increments using. I elected to generate the following metrics:

1) Percentage of landscape (PLand): This metric measures landscape composition and quantifies how much of the landscape is comprised of a particular patch type (or habitat). It is a class level metric.
2) Contrast weighted edge density (CWED): This metric computes the density of all edges in all patches in the landscape weighted by the degree of contrast between adjacent patches. A low level of CWED would indicate a low level of fragmentation, while a high level would indicate high fragmentation within the landscape. CWED increases as the amount of edge in the landscape increases and/or as the contrast in edges involving the corresponding patch type increase (i.e., contrast weight approaches 1). It is a landscape level metric. Weights are determined by the user (low to high), based on the map classification (Table 2).
3) Contagion: It is essentially an index of aggregation at the landscape level. This metric describes the degree of clumping of the landscape into large homogeneous patches. It measures fragmentation based on cell size distribution. A landscape with high Contagion would include regions with large clumps of the same cell type. A low level of Contagion would indicate a disaggregated landscape with many small regions of different adjacent cell types. It is a landscape level metric.

4) Area_AM: Area Weighted Mean Patch Size. This metric describes the area weighted mean patch size across all patch types at the landscape level. It is an index of landscape level fragmentation. It measures the degree to which the landscape is dominated by large patches vs. small patches based on patch size distribution. A high value indicates relatively low levels of fragmentation and dominated by large patches, while low values indicate high levels of fragmentation.

I used a logistic regression modeling framework to identify the predicted probability of marten habitat use, based on comparing habitat variables at sites with marten presence to sites where marten were not detected. Given a binary response variable with a binomial distribution (marten present or non-detected), the study conforms to standard logistic regression. The mathematical model for the logistic function is as follows:

$$P = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_n x_n)}$$

where P is the predicted probability of marten presence for the given combination of covariates (X_i), and slopes (β_1), and the intercept (β_0) are maximum likelihood estimates. In order to investigate factors influencing marten habitat selection, I compared three different sets of models utilizing different scales of habitat relationships: Plot level (90 m), home range (630 m), and across multiple scales using bivariate scaling of habitat variables. This allowed the comparison of three different analyses across different spatial scales.

For the stand, home range, and multiple-scale analysis I used an information-theoretic method based on Kullback-Leibler information, an equation describing the information lost when a model is used to approximate truth (Burnham and Anderson 1998). In order to develop individual models for each spatial scale, I first extensively reviewed previously published studies on the habitat ecology of American martens to determine a set of characteristics that are likely to be important in determining the use or selection of a site at the stand, home range and multiple scales. I then added variables that I hypothesized to have ecological importance to American martens within my study region. In order to limit the number of variables, and thus the number of candidate models, each potential variable was screened based on the following criteria: 1) The variable is relevant to the study region, 2) The variable is measurable, has a high level of precision, and was measured in the field or is available in existing GIS coverages, 3) The variable was identified to be important in a previously published study on American martens or hypothesized to be an important characteristics of forests in the study region, 4) The variable is of likely biological importance to martens, and 5) The variable is evaluated at the appropriate scale (Slauson 2003). All variables meeting the screening criteria were used to develop competing models representing alternative hypotheses for habitat selection at each spatial scale. Conceptual models were then translated into logistic regression models using the selected variables for each scale. The resulting model sets represented competing hypotheses about scale-specific characteristics that drive marten habitat selection. Variables that did not meet these criteria were excluded from further consideration.

Plot Level Analysis

At the plot scale, variables were measured within a 90 m radius around each snare location. For each set of predictor variables I developed logistic regression models using the selected variables for this scale. Each model represented a plausible mechanism whereby predictor variables may determine marten presence. Only variables that had a significant univariate Wilcoxon Rank Sum Score (p-value <0.05) at the plot level (90 m) scale were included. Variables selected for inclusion in candidate models at the plot level (90 m) are presented in Table 3. Explanatory variables at the plot scale included structural, compositional, and topographic characteristics of stands.

For the plot level analysis, I chose two landscape composition variables, PLand of Large sawtimber and PLand of Seedling/sapling, both of which were significantly related to marten occurrence based on the univariate analyses. Several studies on martens have shown close association with later seral stages (e.g. Buskirk 1984; Buskirk and Powell 1994; Campbell 1979; Slough 1989) and have several life history needs (foraging, resting, denning) that are directly linked to the presence of large live trees, snags, and logs typically most abundant in the later seral stages. Elevation also was a significant univariate predictor, which is not surprising given its strong relationship with microclimate conditions. I chose contrast weighted edge density (CWED) to represent landscape fragmentation, and I chose the All Roads layer to test the effects of roads as a fragmenting feature within stands. Candidate models at the plot level (90 m) used for hypothesis testing and logistic regression modeling are shown in Table 4.

Home Range Analysis

For the home range analysis, variables were measured within a 630 m radius around each snare location, approximately corresponding to the average marten home range in northern Idaho (Tomson 1999). Explanatory variables at the home range scale included structural, compositional, and topographic characteristics found within home ranges. Landscape composition variables were selected based on their univariate significance in predicting marten presence at the 630 m scale (Table 3). At the home range scale (630 m), all vegetation classes were included in candidate models. I selected all vegetation classes in order to describe the stage of stand development and corresponding level of structural diversity within the home range. Chapin et al. (1998) found that marten home ranges contained significantly larger maximum patch sizes of mature forest than would be expected by chance. Topographical Moisture Index was included to test the hypothesis that American martens locate home ranges in relatively mesic habitats, due to microclimate conditions and enhanced productivity. Elevation has a strong influence on the microclimate conditions and was thought to play a role in habitat selection due to the distribution of vegetation types, snow conditions and prey communities along the elevational gradient. CWED is an index of fragmentation and was chosen to evaluate the degree of fragmentation of the landscape by high contrast edges between different patch types. The All roads layer was chosen to test the whether roads act as a fragmenting feature within landscapes which affects the probability of marten occupancy at the home range scale. Candidate models for the home range analysis used for hypothesis testing and logistic regression modeling are shown in Table 5.

Multiple-scale Analysis

The objective of testing alternative models containing variables at multiple scales is to explore whether American marten select habitat features at different scales within this study area. For example, it may be that the factors that are the strongest predictors of marten occupancy at the home range scale and those that predict marten foraging habitat at the 90m scale may be different. Evaluating multiple-scale models enables clear identification of multiple-scale habitat selection, if it exists.

The analysis begins with a univariate scaling analysis, known as bivariate scaling (Thompson and McGarigal 2002), to identify the scale at which each independent variable is most strongly related to marten occurrence. Each variable was subjected to a univariate test of significance at each scale (PROC NPAR1 WAY Wilcoxon; SAS Institute 1999-2000), following Hosmer and Lemeshow (2000). Only variables that had a significant Wilcoxon Rank Sum Score ($p < 0.05$) at at least one scale were retained for the logistic regression modeling. When more than one scale was significant, I selected the scale with the smallest p-value. All other scales of each variable were excluded from further analysis. Next, I eliminated one of each pair of variables with a Pearson's correlation >0.5.

I then evaluated the performance of each variable across all possible models that can be constructed from the pool of remaining independent variables. This entailed evaluating all models that resulted from a factorial combination of all variables that were significant in the bivariate scaling using PROC LOGISTIC (SAS Institute Inc., Cary, NC). This all-models approach is intended not as a model selection step but rather as an additional variable screening step. Importantly, the all models approach provides valuable information about the strength of relationship between each variable and marten occupancy through two related metrics: universality and consistency (Copeland et al. 2007). Universality is the proportion of models in which each variable was significant ($p<0.25$, Hosmer and Lemeshow 2000:95), whereas consistency is the proportion of models in which the slope coefficient had the same sign. A perfectly universal and consistent variable would be significant in all models in which it occurred and would not change sign (Copeland et al. 2007). A variable that has a high degree of universality and consistently predicts presence or non-detection of martens is a strong predictor of marten occurrence.

Variables that passed the universality and consistency test (Table 9) were then used to develop an a priori set of candidate models for further evaluation (Table 10). Explanatory variables in the multiple-scale analysis included structural, compositional, topographic, and landscape pattern characteristics. Seral stage variables PLand of large sawtimber, seedling/sapling, pole sawtimber, and non-stocked areas were universal and consistent predictors of American marten occurrence, and also provided a description of the stage of stand development and corresponding level of structural diversity found to be significant for martens at multiple scales. Landscape level metrics CWED and Contagion were chosen to describe landscape patterns. CWED is an index of fragmentation and was chosen to evaluate the degree to which the landscape is dissected by high contrast edges. Contagion provided an index of aggregation at the landscape level and describes the degree of clumping of the landscape into large homogeneous patches. Large continuous patches of mature forest have been shown to be important for marten habitat selection

(Chapin et al. 1998), and I hypothesized that large homogeneous patches of mature forest would be important for American martens in the IPNF.

Model Selection and Analysis

In this analysis, I compared sets of candidate models at the plot level (90 m), home range scale (630 m), and multiple scale models containing universal and consistent variables. This comparison is intended to evaluate alternative scaling approaches to modeling marten habitat selection. For each set of models, I conducted model selection, analysis, and multi-model inference using information theoretic methods (Burnham and Anderson 2002). These methods identify the optimal balance between model parsimony and accuracy of fit and facilitates simultaneous evaluation of multiple hypotheses. Information-theoretic methods allow direct comparisons of the relative importance of several mechanisms that may affect marten presence in this study landscape as well as facilitate multi-model inference, which can be applied to predict marten presence using models for all mechanisms considered in proportion to their relative importance (Burnham and Anderson 2002).

I ranked each set of models separately using Akaike's Information Criterion (AIC). AIC is an equation that estimates Kullback-Liebler information, an equation describing the information lost when a model is used to approximate truth (Burnham and Anderson 1998). AIC has two components, one that assesses lack of fit and a second that penalizes for each additional parameter by increasing the AIC value. Therefore, when comparing a set of candidate models, models with the lowest AIC values provide the strongest inference given the data and the set of a priori models (Anderson et al. 2000). I used the Akaike's information criterion for small sample sizes, AICc, recommended for use when the sample size divided the total number of parameters is <40 (Burnham and Anderson 1998). Models were interpreted by the comparison of ΔAIC_c values, where

$\Delta AIC_c = AIC_c - \text{minimum } AIC_c$

Using ΔAIC_c (Δi) values provides a measure of strength of evidence and a scaled ranking for candidate models (Anderson et al. 2000). Models with $\Delta AIC_c < 2$ are strongly supported and should be considered when making inferences about the data. Models with ΔAIC_c values between 2 and 7 have less support, and those with $\Delta AIC_c > 10$ have little or no support (Burnham and Anderson 1998). To further interpret the relative importance of a model, Akaike's weights (w_i) are used. ΔAIC_c values are used to compute w_i, which is considered the weight of evidence in favor of a model being the best approximating model given the model set (Burnham and Anderson 2002). Unless the model with the lowest AIC_c value has a w_i of >0.9, then other models should be considered when drawing inferences about the data (Burnham and Anderson 1998).

In order to compare the results of the stand, home range and multi-scale analyses, I calculated the classification accuracy for the top-ranked model from each of the three analyses. To do so, I randomly split the dataset for each analysis in half to generate model building and testing subsets. I then generated new model coefficients using the model building subset. I then determined the cutpoint (e.g., predicted probability of presence) that maximized the classification accuracy for both the presence and non-detection sites. Using the same model coefficients and cutpoint, I then determined the classification accuracy for the model testing subsets. This approach provides an unbiased and easily interpreted estimate of the predictive power of the models produced by each of the three analyses. This approach is similar to calculating the area under the Receiver Operator Curve (Pearce and Ferrier 2000).

RESULTS

Survey Results

Over the three winter seasons of 2004, 2005, and 2006, I surveyed a total of 569 locations. *Martes americana* were detected at 152 individual snare locations and *Martes pennanti* were detected at 19 individual stations. For habitat modeling, only data from the winters of 2005 and 2006 were included due to differences in sample procedures between the winter of 2004 and the winters of 2005 and 2006. Over the winter seasons of 2005 and 2006, 287 locations were surveyed

Genetic Results

Using diagnostic restriction enzyme patterns on a region of cytochrome b, *Martes americana* were detected at 110 individual hair snare stations.

Habitat Models

I used a logistic regression framework to investigate the relationships between American marten presence and a suite of habitat variables that were identified *a priori* on the basis of previous research. My primary goal was to model habitat use for American marten in northern Idaho.

Plot Level Analysis

At the plot level (90 m), based on the ΔAIC (Δi) values for AIC and the Akaike weights (w_i), there were four top models that stand out as the best of the candidate set containing 16 models (Table 6). Models 1, 2, 3,and 4 contained variables that were significant indicators of marten habitat selection. The top model is Model 1 (AIC= 366.48, Δi=0.00, w_i=0.259), and contained seral stage variables Large Sawtimber and Seedling/Sapling. Models 2 (Δi=0.019, w_i =0.236), 3 (Δi =0.32, w_i =0.221), and 4 (Δi=0.67, w_i=0.185) were within an ΔAIC < 2 (Table 6). Model 1 is only 1.09 times more likely than model 2 (evidence ratio = w_1/w_2 = 0.259/0.236) to be the best given the data and candidate model set, is 1.17 times more likely to be the best compared to third-ranked model 3 (evidence ratio = 0.259/0.221) and 1.4 times more likely to be the best fourth-ranked model 4 (evidence ratio = 0.259/0.185). However, If I compare the top model to the model that is ranked 6th, I find that model 1 is 212.12 more times likely to be the best (evidence ratio = 0.259/0.00122) than model 6. The evidence ratios imply that while models 1,2,3,and 4 clearly are superior to the other models considered, there is uncertainty about which of models 1,2,3,or 4 is best. The remaining models are unlikely to be the best model as indicated by their Δi values (Δi > 7). In the top ranking Model 1 the seral stage variable PLand of Seedling/Sapling was the most significant contributor (p=0.00094), and has a negative coefficient, indicating a negative influence on marten presence in this study landscape (Table 12). PLand of Seedling/Sapling is consistently a negative indicator of marten presence and is present in all four of the top ranked models. The top 4 models included parameters with coefficients that are not significantly different from zero, indicating that these variables are not significant contributors to marten habitat selection at this particular scale in this study area. The classification accuracy for the top ranked Model 1 was determined to be 73%.

Home Range Analysis

In the home range analysis at 630 m, the global model, Model 1 (AIC=367.02) stood out as the best model out of all candidate models based on ΔAIC (Δ*i*) values for AIC and the Akaike weights (w_i). The global model was the top ranked model out of 23 possible candidate models and there are no other models within a ΔAIC < 2 (Table 7). Model 1 (Δ*i*=0.00, w_i =0.881) is 21.86 times more likely to be the best model than model 2 (evidence ratio = w_1/w_2 = 0.881/0.0403), and 31.17 times more likely to be the best model than model 3 (evidence ratio = w_1/w_3 = 0.881/0.02826). This is strong evidence that the top ranked global model is the best model out of the candidate set. The remaining twenty models are unlikely to be the best models as indicated by their Δ*i* values (Δ*i*>7). In the top ranked global model MI (p=0.00311) was the most highly significant variable, followed by CWED (p=0.00738) and PLand NS (p=0.04539), and all had negative coefficients, indicating a negative influence on marten presence (Table 13). The top model included seven parameters with coefficients that are not significantly different from zero, indicating that these variables are not significant contributors to marten habitat selection at this particular scale in this study area. The classification accuracy for the top ranked global Model 1 was determined to be 70%.

Multiple-scale Analysis

A) Scaling

Bivariate scaling revealed that PLand of Large sawtimber was highly significant at scales 90 m, 180 m, 270 m (Figure 3). PLand of Small sawtimber (Figure 4) and Non-forest (Figure 5) was non-significant to marten presence in the landscape at any scales and therefore, these variables were not considered for inclusion in candidate models (Table 10). PLand of Seedling/Sapling was significant at 180 m, 270 m, and 990 m (Figure 6). Interestingly, PLand of Pole timber was significant at 90 m and 180 m and then became non-significant as scales increased (Figure 7). PLand of Non-stocked (Figure 8) timber stands is a highly significant negative predictor of marten presence at all scales. Results of scaling and metrics are shown in Table 8.

Landscape metrics including Area Weighted Mean Patch Size (AREA_AM), Contrast Weighted Edge Density (CWED), and Contagion were calculated. AREA_AM was a significant predictor of marten presence at 180 m and 270 m (Figure 9). CWED was significant at all scales, and became increasingly significant as scale increased (Figure 10). Contagion was significant across all scales and became increasingly significant as scale increased (Figure 11). Variables extracted from the DEM and used in bivariate scaling were moisture index and elevation. Moisture index was significant at scales above 540 m, and became increasingly more significant as scale increased (Figure 12). Elevation was significant at the 90 m scale only (Figure 13). The All Roads variable was not significant at any scale and it was therefore dropped from further consideration (Table 8). In each of the 12 variables, I used the scale with the lowest P-value.

B) Universality and Consistency

All possible factorial combinations of 12 independent variables produced 2,048 logistic regression models. As each variable could only be present in one-half of the possible models, the analysis of individual variable performance was based on 1,024 models. Recall that Universality is the proportion of models in which each variable was significant ($p<0.25$, Hosmer and Lemeshow 2000:95), whereas Consistency is the proportion of models in which the slope coefficient had the same sign. A final list of predictor variables from bivariate scaling output and univariate tests of significance used in logistic regression modeling is shown in Table 3.

From all the models that were evaluated, there were seven variables that were highly universal and consistent and therefore strongly associated with marten presence (Table 9). These variables are Moisture Index at 900 m, PLand Nonstocked timber at 810 m, PLand Seedling/Sapling at 990 m, CWED at 630 m, PLand Large Sawtimber at 90 m, PLand Pole timber at 90 m, and Contagion at 630 m. Moisture Index and Non-stocked timbered areas were the best variables for distinguishing marten habitat selection. Both these variables were 100% universal and 100% consistently strong negative indicators of marten presence across all logistic regression models (Table 9). American marten negatively responded to Moisture Index at 900 m from sample points (negative coefficient 100% of the time) and Percentage of Landscape (PLand) of Non-stocked timber stands at 810 m (negative coefficient 100% of the time) were significant ($p<0.25$) in all models. Percentage of Landscape of Seedling/Sapling timber class at 990 m was negatively correlated with marten presence (negative coefficient, $p<0.25$ 94% of the time), and CWED at 630 m was also negatively correlated with marten presence (negative coefficient, $p<0.25$ 98% of the time). Contagion at 630 m was 79% universal ($p<0.25$ 79% of the time) and was 100% consistent. Out of 1,024 models, Contagion 630 m was negative in 1,017 models and positive in the remaining 7 models.

Percentage of Landscape of Large Sawtimber and Pole timber were strong positive indicators of marten presence. PLand of Large Sawtimber at 90 m from the sample point was positively correlated with marten presence (positive coefficient, $p<0.25$ 91% of the time), as well as PLand of Pole timber at 90 m from the plot (positive coefficient, $p<0.25$ 96% of the time). All variables were 100% consistent except for Contagion, which was 99.32% consistent. A perfectly consistent and universal variable would be significant in all models in which it occurred and would not change sign.

C) Candidate Models from Universal and Consistent Variables

From the seven universal and consistent variables, six candidate models were produced (Table 10). Based on ΔAIC (Δi) values for AIC and the Akaike weights (wi), there was one top model that stands out as the best of the candidate set. The top ranked model is Model 1 (AIC=359.33), the global model containing the top universal and consistent variables (Δi=0.00, wi=0.951) (Table 11). This model is 29.08 times more likely than the second ranked model 2 (Δi=6.74, wi=0.0327) to be the best model. The remaining five models are unlikely to be the best models as indicated by their Δi values ($\Delta i>7$). In the global model, MI at 900 m (p=0.01004), CWED at 630 m (p=0.0028), and Contagion at 630 m (p=0.01002) all have significantly negative coefficients, while PLand Large Sawtimber (p=0.02081) has a significantly positive coefficient (Table 14). It should be noted that the top model included three parameters with coefficients that are not significantly different from zero. PLand of Seed/Sap (p=0.06368), PLand NS (P = 0.1942) have non-significant negative coefficients. PLand pole (p = 0.07215) has a non-significant positive coefficient. The classification accuracy for the top ranked global Model 1 was determined to be 76%.

DISCUSSION

Scaling

A fundamental concept in animal ecology is that each species occurs within a limited range of environmental conditions, defining its habitat niche (Hutchinson 1957). In the past, most attention has focused on identifying the most important habitat variables. However, in the past several decades it has become evident that identifying the operative scale for these variables is equally important, to the extent that scaling has been proposed as a central question in ecology (Levin 1992). Identifying the proper variables, but at an incorrect scale may lead to weak or incorrect apparent relationships (Wiens 1989). In this analysis, I focused explicitly on evaluating the relationships between marten occupancy and several potentially important environmental variables across a range of spatial scales.

Bivariate scaling (Thompson and McGarigal 2002) has been shown to be a highly effective method for identifying the appropriate scale in species-environment relationships modeling. By evaluating the strength of relationship between each environmental variable and marten occupancy across a range of spatial scales provides a clear indication of the scale at which each variable influences this species. The results of the bivariate scaling showed strong differences among variables in the scales at which they operate, and also show very large differences in the apparent strength of the relationship within each variable. For example, these results indicate that at the finer scale of selecting habitat within home ranges, martens actively select late-seral microhabitat conditions and strongly avoided early-seral open canopy locations. At the home range scale, martens select home ranges that avoided landscapes that contain large areas of early-seral open canopy conditions and are highly fragmented by high contrast edges. Interestingly, this implies avoidance of non-suitable habitat rather than selection for suitable habitat. At multiple scales, martens avoid landscape with large areas of early-seral open canopy that are fragmented by high contrast edges and select for within home range foraging habitat of mid and late-seral forest types.

In this study, I compared three different models utilizing different scales of habitat relationships: Plot level (90 m), home range (630 m), and across multiple scales using bivariate scaling of habitat variables. This provides an explicit framework to consider multiple scale habitat selection in this species. Since animals hierarchically select habitats, it is essential to measure variables across a variety of spatial scales in order to reveal the true grain at which the animal responds within the landscape (Kotliar and Wiens 1990). The scale at which the animal interacts with the environment and responds to levels of fragmentation and habitat patterns will strongly predict species presence and persistence in the landscape. Importantly, the environmental variables of importance and grain of response for some processes, such as establishing home ranges, may differ greatly from the variables and scales of importance for other processes, such as habitat selection for foraging within home ranges. The three modeling efforts across several spatial scales provide an interesting insight into this multiple-scale process of habitat selection for *Martes americana.*

Plot Level Analysis

The top model is Model 1 (Δi=0.00, w_i =0.259), and contained seral stage variables Large Sawtimber and Seedling/Sapling (Table 6). Looking at the significance of each variable I find that PLand of Seedling/Sapling is the most highly significant variable negatively contributing to marten presence (Table 12), and in fact is the only highly significant variable in all top four models. This result is rather surprising given that the bivariate scaling results indicated that PLand Seedling/Sapling is not significantly different at this scale (Figure 6). Thus, PLand of Seedling/Sapling is a strong negative indicator of marten presence, since it is an indicator of open canopy within the landscape. Preferred prey species such as red-backed voles (*Clethrionomys gapperi*) and red squirrels (*Tamaisciurus ruficanus*) are not classically associated with open canopies and are unlikely to be found in open canopy stands. While PLand of Non-stocked timber stands was significant at all scales in the bivariate scaling output (Table 8), Non-stocked was a vegetation class that did not occur in any marten presence sites in my study area, and only occurred in absence sites. Due to this fact, this variable was not included at the plot level (90 m) analysis.

Home Range Analysis

In the home range analysis, the global model containing all 10 variables was clearly the most significant model based on ΔAIC (Δi) values for AIC and the Akaike weights (w_i). In this global model, CWED was the most highly significant variable (p=0.00738), followed by MI (p=0.00311) and PLand NS (p=0.04539). Once again, PLand of Non-stocked timber is an indicator of open canopy. Each of these significant variables had negative coefficients, indicating a strong negative relationship to marten presence, and avoidance by martens of Non-stocked open canopy areas (Table 13). Tomson (1999) documented that martens preferred mature timber stands with average

DBH > 22.9cm, and showed a significant preference for mature timber classes over seedling/sapling classes within his nearby study area encompassing an area within the Cabinet mountain range of northern Idaho. This is consistent with my findings within my study landscape. Mature stands in this landscape are likely providing preferred prey species, as well as access to structures that provide thermal shelter and protection from predators.

Contagion and CWED were more highly significant at the home range scale (630 m) than all other scales that were tested using bivariate scaling. CWED at 630 m was the most significant variable in the top ranked global model, indicating that at the home range scale, martens respond negatively to stands of mature timber juxtaposed next to open canopy areas of non-stocked timber and avoid open canopy areas. These human induced edges create fragmented landscapes that may hinder movement of American martens and create inhospitable habitat. Martens with home ranges in fragmented habitats are more likely to risk predation while traveling through an area lacking escape structures that are frequently found in un-fragmented areas composed of mature forest.

Multiple-scale Analysis

The multi-scale analysis shows that marten presence is positively correlated with the Percentage of the Landscape (PLand) composed of large sawtimber interspersed with stands of pole timber. These variables had positive coefficients at the 90 m scale and focus on the high quality habitat. This suggests that marten actively select habitat based on fine-scale features. This also indicates that late-seral stands are an important component for marten habitat use in the Idaho Panhandle National Forest and this is consistent with results from previous marten habitat studies (Buskirk and Powell 1994; Campbell 1979; Slauson 2003; Soutiere 1979; Stevenson and Major 1982; Wilbert 1992). All of the other variables considered in this analysis have negative coefficients and are at the landscape scale (> 630 m), implying that the negative influences on habitat selection operate at a very different scale than the positive influences on habitat selection. Non-stocked forest stands and young seedling/sapling forest stands were strongly avoided by martens and were negative predictors of marten presence. Thus, a sample site located in a small stand of large sawtimber will not be used by marten if it is embedded within a landscape dominated by fragmented patches.

Interestingly, my results predicted that martens have a negative relationship with Moisture Index, indicating that they occur relatively more commonly on convex upland mountain slopes than in the moist valley riparian areas. This is contrary to many previous studies which typically report martens to be most abundant in highly productive riparian areas. This unexpected result has several potential interpretations. First, the result may be somewhat misleading due to the fact that the areas with the highest moisture index in my study are low elevation areas around Priest Lake that are also highly cut-over forests. Martens were found at only a few plots in this area. This may be due to the effect of forest management in these areas rather than moisture index. Most riparian zones in this study area are narrow with steep slopes rising above. Moisture index would be high only along the very bottom of these narrow riparian zones, and would be quite low even in nearby locations upslope. Thus, martens could actively select for riparian zones, but as the hair snares were set on adjacent uplands with relatively low moisture index, the result could be a spurious negative relationship. This absence of martens in the highest moisture index areas could lead to a spurious negative overall relationship with moisture index in the logistic regression models. The second alternative is that martens, contrary to prevailing expectation, actually are less abundant in the largest riparian zones than on more convex upland slopes. This unexpected result would be interesting. Thirdly, competition with fisher (*Martes pennanti*) and other predators who strongly select habitats in riparian areas could exclude martens from utilizing more mesic sites. However, my impression from observing rates of detection and abundance of tracks in upland and riparian zones is that there didn't seem to be any pattern of more abundance on uplands than in riparian areas. Thus, I am unable to satisfactorily account for this unexpected result with respect to moisture index.

Contrast weighted edge density (CWED) was significant across all scales and most significant at 630 m (Table 8). High edge contrast, such as resulting from extensive juxtaposition of preferred stands of mature timber with seedling/sapling and non-forest, is negatively associated with marten presence; marten avoid landscapes with large amounts of high contrast edges. Fragmentation of habitat (e.g., reduction in patch size, increased isolation of patches, and increased levels of stand edge) is thought to play a major role in marten habitat use (Buskirk and Powell 1994). Additionally, Buskirk and Powell (1994) proposed that the type of habitat associated with both sides of the edge may be more important than the edge itself. For example, a patch of young forest configured next to a late-seral forest would be more likely to be used than the same patch of young forest adjacent to areas of non-forest, non-stocked patches, or a recent clear-cut.

Contagion is the degree of clumping of the landscape into large homogeneous patches and measures fragmentation based on cell size distribution. Contagion was significant at all scales (Table 8), as well as in the top ranked global model 1 at 630 m (Tables 11 & 14). A homogeneous landscape composed of patches of mature large sawtimber is an important component of marten habitat selection, as patch configuration is important to martens. A landscape where like patch types are highly clumped together significantly predicts marten presence in the Idaho Panhandle National Forest. Studies in Maine have found that the patch size used by martens (2.7 ha) was significantly larger than unused patches (1.5 ha) (Chapin et al. 1998). Used patches were significantly closer to a patch greater than 2.7 ha than were unused patches. A significant relationship was also found between used patches and the distance to the nearest forest preserve. Chapin et al. (1998) concluded that patch area was the single most important factor that affected habitat use by marten in their study area.

Comparing all 3 sets of models

Characterizing the landscape surrounding each point at multiple scales enabled me to select the appropriate scale(s) at which each aspect of landscape composition was most significant for *Martes americana*. At the plot level (90 m) stands containing seedling/sapling vegetation type were highly avoided by martens. At the home range scale, seral stage, and fragmentation of the landscape were the best predictors of marten presence. CWED and Non-stocked areas were important negative predictors of marten habitat selection in this landscape. Martens negatively responded to a high amount of edge contrast in this landscape. When stands of preferred habitat of larger and older forest are adjacent to non-stocked timber stands, this fragments the landscape and makes it inhospitable marten habitat.

Using bivariate scaling analysis of universal and consistent variables in the multiple-scale approach, the strongest and most informative model was model 1, the global model (AIC = 359.33). This model was also more highly supported than any of the candidate models at the plot level (90 m) and home range (630 m) level, and consequently also had the highest classification accuracy. This shows the superiority of the multi-scale approach to the plot and the home-range models. In this multi-scale model, four out of seven variables included in the model have coefficients that were significantly different from zero; two were nearly significant (PLand Seedling/Sapling p=0.06, and PLand Pole timber p=0.07), and only one variable was not significantly different from zero (PLand Non-stocked timber p=0.19) (Table 14). This is in stark contrast to the best models produced by the plot level and home range analyses. For both the plot and home range scale models, most of the variables had coefficients that were not significantly different from zero. This suggests that these models are less reliable than the multiple-scale model. This is support for using bivariate scaling and statistics to find universal and consistent variables out of a set of a priori hypothesized variables to include in habitat modeling of this species.

Martes americana in the Idaho Panhandle National Forest are selecting habitats that fulfill their life history needs. Preferred prey species such as red-backed voles (*Clethrionomys gapperi*) and red squirrels (*Tamaisciurus ruficanus*) are closely associated with late-seral mature timber stands and are important determinants of marten habitat selection. Tomson (1999) found that forested stands had significantly higher densities of small mammals than non-forested stands in his study area of the Cabinet Mountains in northern Idaho. He also documented that predation rates on martens were much higher in fragmented regions of the study area and that martens avoided open canopies to avoid predators.

Although elevation was not a highly significant variable in the top habitat models for American martens in the IPNF, it is an interesting variable to examine as it influences vegetation gradients within the landscape. It should be noted that there were few snares set below 800 m due to unsuitable habitat types present at elevations below this cutoff point. Mean elevation for marten presence was 1268.736m. If martens are significantly more abundant at middle elevations this could lead to a non-significance of elevation in the logistic model, which included elevation as a linear gradient.

I hypothesize that martens in the IPNF are responding to both vegetation types and snow depth found at medium and high elevations. Both vegetation type and snow depth will influence available prey and hunting conditions for martens, as well as trees available for resting and coarse woody debris structure. The dominant forest types found at middle elevations are middle montane mesic types composed of engelman spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis)*, and western red cedar (*Thuja plicata)* on north aspects, and larch (*Larix occidentalis*), douglas fir (*Pseudotsuga menziesii)*, white pine (*Pinus monticola*), and some cedar (*Thuja plicata)* found on southerly aspects. In the higher elevational band, forest type is dominated by subalpine fir (*Abies lasiocarpa*), engelman spruce (*Picea engelmannii*), and western hemlock (*Tsuga heterophylla)*. Trees available at higher elevations are inherently smaller in DBH due to harsh growing conditions (e.g. high snow level, strong winds, short growing season etc.) typically found in the subalpine zone.

CONCLUSION

Bivariate scaling coupled with an assessment of universal and consistent variables was very useful in identifying the appropriate scale at which martens respond to habitat heterogeneity in this study area. The strength of this approach is its ability to evaluate the universality and consistency of variable importance across scales in multiple models. This gives a strong indication of the strength of the variables and nature of the influence (positive or negative). A variable that contributed significantly and with a consistent sign would be considered a strong factor predicting marten presence. In this study, evaluating marten habitat relationships across multiple scales was extremely valuable in describing selection of fine scale habitat variables versus coarse scale variables that compose optimal habitat for American marten. The scale of each variable at which martens responded most strongly was important and differed greatly across scales and predictor variables. The scale at which martens are selecting for high quality habitat elements varied greatly from the scale in which they avoided negative elements.

American marten in this study area of the Idaho Panhandle National Forest are selecting stands composed of areas of large sawtimber interspersed with pole timber, and avoiding landscapes with high Contrast Weighted Edge Density (CWED) among cover types and large areas of seedling/saplings or non-stocked areas (e.g. areas that have been harvested but are not regenerating). Pole timber becomes non-significant at scales above 180 m. Pole timber is the most widely spread seral stage found in the Purcell and Cabinet mountain ranges surveyed in my study landscape, and is proportionately more available than mature large sawtimber stands. It is possible that habitat quality in my study area is exceptional and very productive so that martens may fulfill their life history needs with stands of large sawtimber perforated with pole timber. Previous studies in this region have shown that martens use both mature and intermediate (small sawtimber and pole timber) DBH size classes to satisfy all life history requirements because a home range likely encompasses an area that contains these classes (Tomson 1999). This is consistent with my findings in my study landscape. Martens are selecting areas associated with older, coniferous stands with complex physical structure that provides protection from predators, access to prey, and protective thermal microenvironments important for winter survival. Martens are avoiding openings such as clearcuts, non-stocked areas, seedling/sapling stands, and meadows, especially during winter (Koehler and Hornocker 1977; Soutiere 1979; Simon 1980; Tomson 1999). Martens may use some of these openings in the summer if they provide adequate cover and food.

Martens had a strong negative response to patches of seedling/sapling timber at the landscape scale (990 m). Landscapes and patches characterized by non-stocked timber were also strong negative predictors of marten presence across all scales and in the top ranked model 1 (Table 11). From this model, I can infer that martens in this study area in northern Idaho prefer stands of Large sawtimber interspersed with of pole timber at the plot level (90 m), and strongly avoid areas of Non-stocked timber stands (810 m) and areas of Seedling/sapling (990 m) at the landscape scale. A landscape comprised of homogeneous patches of large sawtimber that is aggregated and not fragmented by patches of open canopy appears to be the optimal landscape-level habitat condition in my study area in northern Idaho. Juxtaposing patches of large sawtimber with high contrast cover types such as seedling/sapling or non-forest areas reduces habitat quality, as martens strongly avoid these open canopy areas and the edges created by this juxtaposition substantially reduces the probability of marten detection. Spatial arrangement of preferred habitat is important.

Habitat fragmentation is considered an important process affecting species persistence and predicting species decline (Fahrig 1997). Habitat fragmentation in addition to habitat loss has been shown to have a greater impact on a species than that predicted strictly by habitat loss alone (Fahrig 2002; Pulliam et al. 1992; Saunders et al. 1991). Conservation approaches must consider not only the preservation of sufficient habitat, but also the spatial arrangement of habitat patches across the landscape (Lamberson et al. 1994; Pulliam et al 1992). This study shows that fragmentation of habitat patches can have a dramatic effect on marten presence in the Idaho Panhandle National Forest. Fragmentation of forests in the IPNF create large amount of edge habitat that in turn reduces interior core habitat important for habitat specialized old-growth associated species such as American marten (Andren 1994; Hargis et al. 1999; Thomas et al. 1990). American marten are particularly susceptible to timber harvesting which removes canopy cover, reduces coarse woody debris (CWD), changes mesic sites into xeric sites, removes riparian dispersal zones, and changes prey communities (Buskirk and Ruggiero 1994). Short-term effects of intensive logging include avoidance of clear-cuts and areas with little canopy cover, increased rates of trapping as overhead cover is removed, and higher predation rates. Long-term effects include loss of habitat and fragmentation that results in isolated populations that may eventually become extirpated (Thompson and Harestad 1994). A study by Hargis et al. (1999) in Utah found that martens respond to small amounts of forest fragmentation. A low level of fragmentation was defined as a habitat where forest cover was still the primary landscape component, percent cover ranged from 2% to 42%, and forest connectivity was maintained. Martens rarely used sites where more than 25% of an area was removed. No martens were captured in areas where there was less than 100 m between open areas, again underscoring the fact that highly contrasted edges and areas of open canopy are highly avoided by American marten.

Management Implications

Martes americana in the Idaho Panhandle National Forest prefer late-seral mature stands for resting and denning, as well as capturing preferred prey species that are associated with mature late-successional stands, such as red-backed voles (*Clethrionomys gapperi*) and red squirrels (*Tamaisciurus ruficanus*). These stands should not be perforated with patches of seedling/sapling or non-stocked areas, as martens highly avoid these areas, consistent with the findings of Hargis et al.(1999) for temperate forests in Utah as well as Tomson (1999) in northern Idaho. Marten appear to actively avoid landscapes with relatively high areas of seedling/sapling and nonstocked conditions at the home range scale. Therefore, optimal marten habitat would consist of landscapes dominated by mature forest, with relatively low areas of seedling/sapling and non-stocked stands, and low overall contrast weighted edge density. Stands should be configured in a homogenous pattern rather than a patch mosaic, as martens negatively respond to high contrast edges and disaggregated patch types. Maintaining connectivity between patches of favorable habitat is important to the persistence of marten populations. Increasing fragmentation reduces habitat connectivity, decreases dispersal success (Doak et al. 1992; King and With 2002), initiates genetic isolation (Gerlach and

Musolf 2000; Gibbs 2001; Young and Clarke 2001), and increases extinction vulnerability (Adler and Nuernberger 1994; Fahrig and Merriam 1985; Kareiva and Wennergren 1995; Lamberson et al. 1994). Harvest pattern in the IPNF has resulted in relatively high levels of fragmentation for much of the remaining late-seral forests. Timber harvest activity should leave large diameter snags as well as other coarse woody debris in place. Structural complexity at the ground created by snags and other downed woody debris is important for martens for a variety of reasons, including resting, denning, and hunting. My results suggest that additional harvest of old-growth and mature forest in the Idaho Panhandle National Forest will reduce marten habitat, and consequently marten populations, by both reducing the preferred habitat (mature and old-growth forest) and increasing avoided habitats (seedling/sapling, nonstocked, and high contrast landscapes).

CHAPTER 1: TABLES

Table 1: Vegetation and timber classification on both state and federal lands in the Idaho Panhandle Nat'l Forest. Seral stage is presented with Diameter at Breast Height (DBH).

Seral Stage based on Diameter at Breast Height (DBH)

Class	**Description**
1. Large Sawtimber	Dominant and codominant trees with DBH > 16 in
2. Small Sawtimber	Dominant and codominant tress with DBH 8-16 in
3. Pole Timber	Dominant and codominant trees with DBH 3-7.9 in
4. Seedling/Sapling	Crop trees< 4.5 ft and < 3 in DBH (open canopy)
5. Non-stocked	Forest land less than 10% stocked with growing stock trees
6. Non-forest	Non-forested areas

Table 2: Contrast Weighted Edge Density file used in FRAGSTATS for weighting. Weights are the dissimilarity between patch types and are scaled 0-1.

Class		**Weight**					
		1	**2**	**3**	**4**	**5**	**6**
Large Sawtimber	**1**	0					
Small Sawtimber	**2**	0.2	0				
Pole timber	**3**	0.4	0.2	0			
Seedling/Sapling	**4**	0.6	0.4	0.2	0		
Non-stocked	**5**	0.8	0.6	0.4	0.2	0	
Non-forest	**6**	1	0.8	0.6	0.4	0.2	0

Table 3: List of predictor variables used in candidate models for the Plot level (90 m), Home Range level (630 m) and Multi-scale analyses. A description of each variable is provided. **X's** Denote variable was used in the analysis at that particular scale.

Variable	**90 m**	**630 m**	**Multi-scale**	**Description**
1) Moisture Index		**X**	**X**	•Moisture Index
2) All Roads	**X**	**X**	**X**	•All maintained and unmaintained FS & County roads plus decommissioned, grown over & un-drivable roads that may still provide movement corridors for animals.
3) Elevation	**X**	**X**	**X**	•Elevation at X scale from sample point
4) Contagion			**X**	•An index of aggregation or clumping at the landscape level
5) CWED	**X**	**X**	**X**	•Contrast Weighted Edge Density
6) AREA_AM			**X**	•Area Weighted Mean Patch Size
7) Percentage of Landscape Large Sawtimber	**X**	**X**	**X**	•Percentage of landscape comprised of Large Sawtimber (>16 in)
8) Percentage of Landscape Small Sawtimber		**X**	**X**	•Percentage of landscape comprised of Small Sawtimber (8-16 in)
9) Percentage of Landscape of Seedling/Sapling	**X**	**X**	**X**	•Percentage of landscape comprised of Seedling/Sapling (< 4.5 ft and < 3 in DBH)
10) Percentage of Landscape of Pole timber type		**X**	**X**	•Percentage of landscape comprised of Pole timber (3-7.9 in)

11) Percentage of Landscape of Non-stocked areas	**X**	**X**	•Percentage of landscape comprised of Non-stocked areas (Areas stocked below minimum levels needed to meet FPA requirements
12) Percentage of Landscape of Non-forest	**X**	**X**	•Percentage of landscape comprised of Non-forest areas

Table 4: Set of candidate models at the Plot level (90 m). K is number of parameters. Variables were selected for model inclusion was based on univariate analysis. A total of 16 models were tested.

Model #	**K**	**Model**
1	2	LG + SS
2	3	Elev + LG + SS
3	1	SS
4	2	ELEV + SS
5	5	Global
6	2	Elev + LG
7	3	Elev + LG + CWED
8	1	LG
9	3	Elev + LG + AR
10	2	LG + CWED
11	3	LG + AR + CWED
12	2	LG + AR
13	1	Elev
14	2	Elev + AR
15	2	Elev + CWED
16	3	Elev + AR + CWED

Elev = Elevation at 90m, LG =PLand of Large Sawtimber at 90m, SS = PLand Seedling/sapling timber at 90m, CWED = Contrast Weighted Edge Density 90m, AR = All Roads 90m.

Table 5: Set of candidate models at the Home Range level (630 m). K is number of parameters. Variables were selected for model inclusion was based on univariate analysis. There were 23 total models tested.

Model #	**K**	**Model**
1	10	Global
2	1	MI
3	2	MI+SS
4	2	MI+LG
5	2	MI+Elev
6	3	SS + NS + NF
7	2	Elev + CWED
8	3	Elev + LG + CWED
9	6	LG+SM+Pole+SS+NS+NF
10	2	LG + CWED
11	3	Elev + AR + CWED
12	3	Elev + SS
13	1	Elev
14	1	SS
15	2	Elev + AR
16	2	Elev + LG
17	3	Elev + LG + SS
18	3	LG + AR + CWED
19	2	LG + SS
20	3	Elev + LG + AR
21	1	LG
22	2	LG + SM
23	2	LG + AR

Elev = Elevation at 630 m, MI= Moisture Index 630m, CWED= Contrast Weighted Edge Density at 630m, AR = All Roads, LG = PLand of Large Sawtimber at 630m, SM = PLand of Small Sawtimber at 630m, SS= PLand of Seedling/sapling timber at 630m, Pole= PLand of Pole timber at 630m, NS = PLand of Nonstocked timber at 630m, NF = PLand of Non-forest at 630m.

Table 6: Candidate models at the plot level (90 m) sorted by AIC. AIC, ΔAIC, and AIC weights (w_i) are shown. K is number of parameters. Top models with AIC<2 are highlighted. Models below the dashed line represent models that were not significant ($p<0.05$).

Model #	K	Variables	AIC	Δ AIC	w_i
1	**2**	**LG + SS**	**366.48**	**0**	**0.259784**
2	**3**	**Elev + LG + SS**	**366.67**	**0.19**	**0.23624**
3	**1**	**SS**	**366.80**	**0.32**	**0.221373**
4	**2**	**ELEV + SS**	**367.15**	**0.67**	**0.185833**
5	5	Global	368.56	2.08	0.091822
6	2	Elev + LG	377.20	10.72	0.001221
7	3	Elev + LG + CWED	377.32	10.84	0.00115
8	1	LG	378.55	12.07	0.000622
9	3	Elev + LG + AR	378.72	12.24	0.000571
10	2	LG + CWED	378.78	12.3	0.000554
11	3	LG + AR + CWED	379.14	12.66	0.000463
12	2	LG + AR	379.61	13.13	0.000366
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13	1	Elev	381.77	15.29	0.000319
14	2	Elev + AR	383.72	17.24	0.000299
15	2	Elev + CWED	382.28	15.8	0.000287
16	3	Elev + AR + CWED	384.06	17.58	0.000242

Elev = Elevation at 90m, LG =PLand of Large Sawtimber at 90m, SS = PLand Seedling/sapling timber at 90m, CWED = Contrast Weighted Edge Density 90m, AR = All Roads 90m.

Table 7: Candidate models at the Home Range scale (630 m). AIC, Δ AIC, and AIC weights (w_i) are shown. K is number of parameters. Top model with AIC<2 is highlighted. Models below the dashed line represent models that were not significant ($p<0.05$).

Model #	K	Model	AIC	Δ AIC	*wi*
1	**10**	**Global**	**367.02**	**0**	**0.881432**
2	1	MI	373.19	6.17	0.040308
3	2	MI+SS	373.90	6.88	0.028263
4	2	MI+LG	374.61	7.59	0.019817
5	2	MI+Elev	375.19	8.17	0.014828
6	3	SS + NS + NF	375.95	8.93	0.010141
7	2	Elev + CWED	378.78	11.76	0.002463
8	3	Elev + LG + CWED	380.36	13.34	0.001118
9	6	LG+SM+Pole+SS+NS+NF	380.42	13.40	0.001085
10	2	LG + CWED	381.8	14.78	0.000544
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11	3	Elev + AR + CWED	380.76	13.74	0.000912
12	3	Elev + SS	381.64	14.62	0.000587
13	1	Elev	381.65	14.63	0.000584
14	1	SS	382.36	15.34	0.000410
15	2	Elev + AR	382.63	15.61	0.000358
16	2	Elev + LG	383.28	16.26	0.000259
17	3	Elev + LG + SS	383.41	16.39	0.000242
18	3	LG + AR + CWED	383.74	16.72	0.000205
19	2	LG + SS	384.10	17.08	0.000172
20	3	Elev + LG + AR	384.37	17.35	0.000150
21	1	LG	384.68	17.66	0.000128
22	2	LG + SM	385.26	18.24	9.61E-05
23	2	LG + AR	385.49	18.47	8.56E-05

Elev= Elevation at 630m, MI= Moisture Index 630m, CWED= Contrast Weighted Edge Density at 630m, AR = All Roads, LG = PLand of Large Sawtimber at 630m, SM = PLand of Small Sawtimber at 630m, SS= PLand of Seedling/sapling timber at 630m, Pole= PLand of Pole timber at 630m, NS = PLand of Nonstocked timber at 630m, NF = PLand of Non-forest at 630m.

Table 8: P-values of Bivariate Scaling output of variables by Wilcoxon Rank Sum Scores raked by presence/non-detection (p=0.05). Most highly significant scales are highlighted for each variable. Scales are in meters.

Wilcoxon Rank Sum Scores

Scale (m)	PLand of LG SAW	PLand of SM SAW	PLand of SEED/SAP	PLand of Pole	PLand of Non-forest	PLand of Non-stocked
90	**0.004****	0.083	0.283	0.037**	0.2	0.01
180	0.0065	0.192	0.005	0.048	0.36	0.02
270	0.018	0.304	0.001	0.147	0.48	0.006
360	0.058	0.443	0.059	0.053	0.45	0.002
450	0.127	0.482	0.116	0.149	0.36	0.015
540	0.184	0.376	0.156	0.129	0.383	0.011
630	0.25	0.314	0.149	0.172	0.487	0.003
720	0.268	0.261	0.075	0.258	0.44	0.003
810	0.259	0.277	0.14	0.3	0.494	**0.002****
900	0.0265	0.271	0.073	0.342	0.405	0.004
990	0.285	0.256	**0.000****	0.37	0.449	0.002
1080	0.284	0.217	0.242	0.404	0.376	0.003

Scale (m)	AREA_AM	Contagion	CWED	Moisture Index	Elevation	All Roads	
90	0.1127	0.035	0.035	0.08	**0.05****	scale (m)	p-value
180	0.016	0.026	0.036	0.18	0.07	180	0.14
270	**0.013****	0.013	0.013	0.27	0.07	360	0.36
360	0.11	0.013	0.013	0.09	0.07	540	0.27
450	0.36	0.01	0.012	0.09	0.07	720	0.13
540	0.47	0.007	0.006	0.04	0.06	900	0.11
630	0.19	**0.004****	**0.004****	0.02	0.06	1080	0.09
720	0.41	0.006	0.006	0.01	0.06	1260	0.08
810	0.47	0.005	0.005	0.01	0.063	1440	0.09
900	0.46	0.005	0.005	**0.006****	0.06	1620	0.08
990	0.485	0.006	0.006	0.008	0.07	1800	0.07
1080	0.452	0.01	0.014	0.008	0.07	1980	0.07

Table 9: Variables that were highly consistent (>99%) and universal throughout the factorial combination of all models. There were a total of 2, 048 models in a mirrored matrix therefore I evaluated 1,024 models. Coefficients of each variable, proportion of times each variable was significant, number of models and the percentage each variable was either positive or negative.

Variable Code	Variable Name and Scale	Universality (Prop Sig<0.25)	Models Positive	Models Negative	% Consistency
	Model Intercept				
MI	Moisture Index 900 m	1.00	0	1024	100
NS	PLand Non-Stocked 810 m	1.00	0	1024	100
CW	CWED 630	0.98	0	1024	100
P	PLand Pole 90 m	0.96	1024	0	100
SS	PLand Seed/Sap 990 m	0.94	0	1024	100
LG	PLand Large 90 m	0.91	1024	0	100
CO	Contagion 630 m	0.79	7	1017	99.32

MI= Moisture Index at 900m, NS= Nonstocked timber at 810m, CW= Contrast Weighted Edge Density at 630m, P = PLand of Pole timber at 90m, SS = PLand of Seedling/sapling timber at 990m, LG= PLand of Large Sawtimber at 90m, CO= Contagion at 630m.

Table 10: Candidate Multiple-Scale models based on variables screened with Universality and Consistency. K is number of parameters.

Model #	K	MODEL
1	7	Global
2	5	MI + LG + SS + Pole + NS
3	5	CO + LG + SS + Pole + NS
4	4	LG + SS + Pole + NS
5	5	CWED + LG + SS + Pole + NS
6	2	LG + NS

MI= Moisture Index at 900m, CO= Contagion at 630m NS= Nonstocked timber at 810m, CW= Contrast Weighted Edge Density at 630m, P = PLand of Pole timber at 90m, SS = PLand of Seedling/sapling timber at 990m, LG = PLand of Large Sawtimber at 90m.

Table 11: Significant Multiple-Scale Universal and Consistent candidate models sorted by AIC. AIC and ΔAIC. AIC weights (w_i)are shown. K is number of parameters. Top model with AIC<2 is highlighted.

Model #	(K)	MODEL	AIC	Δ AIC	w_i
1	**7**	**Global**	**359.33**	**0**	**0.951627**
2	5	MI + LG + SS + Pole + NS	366.07	6.74	0.032726
3	5	CO + LG + SS + Pole + NS	369.77	10.44	0.005146
4	4	LG + SS + Pole + NS	369.81	10.48	0.005044
5	5	CWED + LG + SS + Pole + NS	369.93	10.60	0.004750
6	2	LG + NS	373.74	14.41	0.000707

MI= Moisture Index at 900m, CO= Contagion at 630m NS= Nonstocked timber at 810m, CW= Contrast Weighted Edge Density at 630m, P = PLand of Pole timber at 90m, SS = PLand of Seedling/sapling timber at 990m, LG = PLand of Large Sawtimber at 90m.

Table 12: Most highly supported models and coefficients from significant candidate models for Plot Level (90m) analysis. AIC, ΔAIC and w_i are shown. Top ranked model and models with Δ AIC < 2 are shown. (** denotes highly significant variables in each model).

Model					**AIC**	**Δ AIC**	***wi***
Large Sawtimber + Seedling/Sapling							
Coefficients:							
	Estimate	Std. Error	z	Pr(>|z|)	366.48	0	0.259784
(Intercept)	-0.419898	0.225036	-1.866	0.06205			
PLand LG	4.65E-03	3.06E-03	1.519	0.12876			
PLand Seed/Sap	-2.21E-02	6.67E-03	-3.308	**0.00094** **			
Elevation+ Large Sawtimber + Seedling/Sapling							
Coefficients:							
	Estimate	Std. Error	z	Pr(>|z|)	366.67	0.19	0.23624
(Intercept)	-1.357519	0.737307	-1.841	0.06559			
Elevation	0.00074	0.000552	1.34	0.18021			
PLand LG	0.004822	0.003071	1.57	0.11643			
PLand Seed/Sap	-0.021047	0.006685	-3.149	**0.00164** **			
Seedling/Sapling							
Coefficients:							
	Estimate	Std. Error	z	Pr(>|z|)	366.8	0.32	0.221373
(Intercept)	-0.157605	0.141459	-1.114	0.26522			
PLand Seed/Sap	-0.023767	0.006484	-3.666	**0.000247** **			
Elevation + Seedling/Sapling							
Coefficients:							
	Estimate	Std. Error	z	Pr(>|z|)	367.15	0.67	0.185833
(Intercept)	-1.038779	0.703787	-1.476	0.139948			
Elevation	0.000703	0.000549	1.28	0.20055			
PLand Seed/Sap	-0.022866	0.00649	-3.523	**0.000426** **			

Elevation= Elevation at 90m, PLand LG = Percentage of Landscape comprised of Large Sawtimber at 90m, PLand Seed/Sap= Percentage of Landscape comprised of Seedling/sapling timber at 90m.

Table 13: Most highly supported models and coefficients from significant candidate models for the Home Range level (630 m). AIC, ΔAIC and *wi* are shown. Top ranked model and models with Δ AIC < 2 are shown. (** denotes highly significant variables in each model).

Model

Global					**AIC**	**Δ AIC**	***wi***
Coefficients:							
	Estimate	Std.Error	z	Pr(>|z|)	367.02	0	0.8814
(Intercept)	1.20E+00	1.51E+00	0.796	0.42604			
CWED	-3.96E-02	1.48E-02	-2.679	**0.00738****			
Elev	-3.65E-04	7.10E-04	-0.514	0.60708			
MI	-9.74E+00	3.30E+00	-2.957	**0.00311****			
All Roads	-9.25E+02	1.98E+03	-0.466	0.64121			
PLand LG.	1.05E-02	1.14E-02	0.918	0.35842			
PLand Small	1.28E-02	1.16E-02	1.107	0.26822			
PLand Pole	1.68E-02	1.31E-02	1.287	0.1982			
PLand Seed/Sap	-5.29E-03	1.08E-02	-0.492	0.62269			
PLand NS	-3.44E-01	1.72E-01	-2.001	**0.04539****			
PLand NF	-2.94E-02	3.44E-02	-0.853	0.39346			

Elev= Elevation at 630m, MI= Moisture Index 630m, CWED= Contrast Weighted Edge Density at 630m, AR = All Roads, PLand LG = Percentage of Landscape comprised of Large Sawtimber at 630m, PLand SM = Percentage of Landscape comprised of Small Sawtimber at 630m, PLand SS= Percentage of Landscape comprised of Seedling/sapling timber at 630m, PLand Pole= Percentage of Landscape comprised of Pole timber at 630m, PLand NS = Percentage of Landscape comprised of Nonstocked timber at 630m, PLand NF = Percentage of Landscape comprised of Non-forest at 630m.

Table 14: Most highly supported model and coefficients from significant candidate Multiple-scale models for universal and consistent variables. AIC, ΔAIC and wi are shown. Top ranked model and models with Δ AIC < 2 are shown. (** denotes highly significant variables in each model).

Model **Global**	Estimate	Std. Error	z	Pr(>|z|)	**AIC**	**ΔAIC**	***wi***
					359.33	0	0.95163
(Intercept)	3.9666	1.22778	3.231	0.00123			
MI 900	-1.957	0.76015	-2.575	0.01004**			
Contagion 630	-0.0331	0.01286	-2.575	0.01002**			
CWED 630	-0.0514	0.01721	-2.989	0.0028**			
PLand LG 90	0.00806	0.00349	2.312	0.02081**			
PLand Seed/Sap990	-0.0135	0.00729	-1.854	0.06368			
PLand Pole 90	0.01194	0.00664	1.798	0.07215			
PLand NS 810	-0.1309	0.10085	-1.298	0.19422			

MI= Moisture Index 900m, CWED= Contrast Weighted Edge Density at 630m, PLand LG = Percentage of Landscape comprised of Large Sawtimber at 90m, PLand SS= Percentage of Landscape comprised of Seedling/sapling timber at 990m, PLand Pole= Percentage of Landscape comprised of Pole timber at 90m, PLand NS = Percentage of Landscape comprised of Nonstocked timber at 810m.

CHAPTER 1: FIGURES

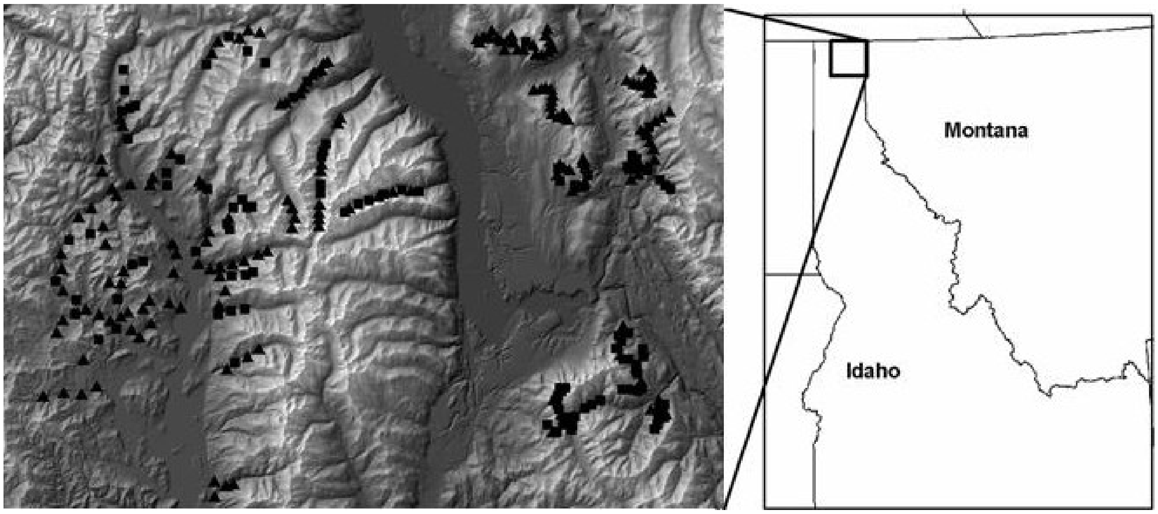

Figure 1: Detailed picture of study area located in the panhandle of northern Idaho visualized on a Digital Elevation Map (DEM). This details the Selkirk Mountain range to the west, the Purcell Mountain range to the east, and the Cabinet Mountain range in the southeast corner of this map. The Kootenai River runs between theses ranges.

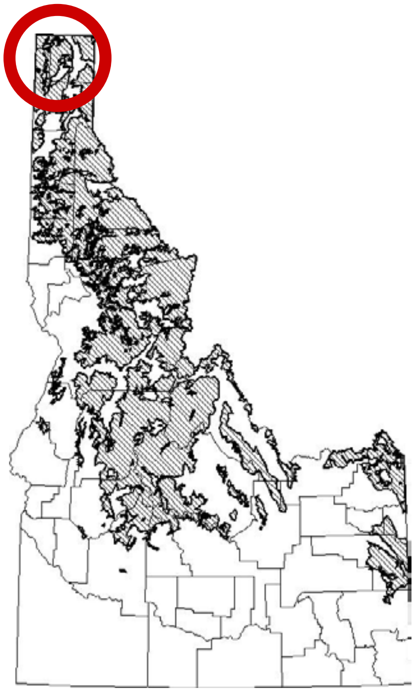

Figure 2: The shaded areas in this map show the historical distribution of *Martes americana* across the state of Idaho. The circled area denotes my study area located in the panhandle of northern Idaho within the Idaho Panhandle National Forest.

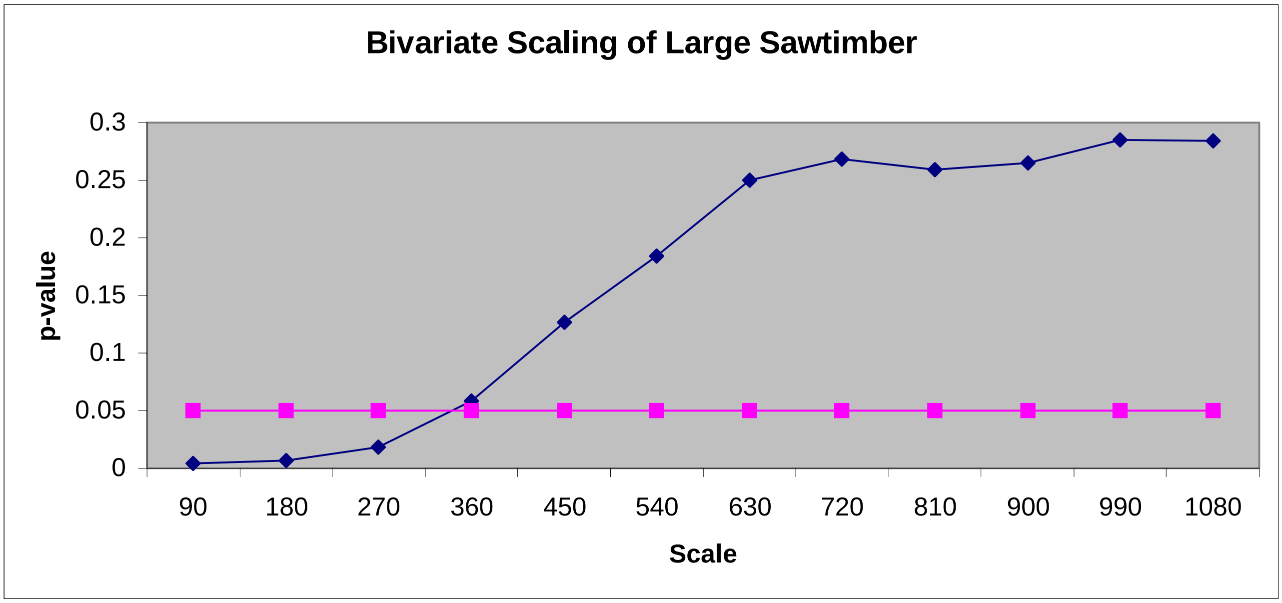

Figure 3: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Large sawtimber at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

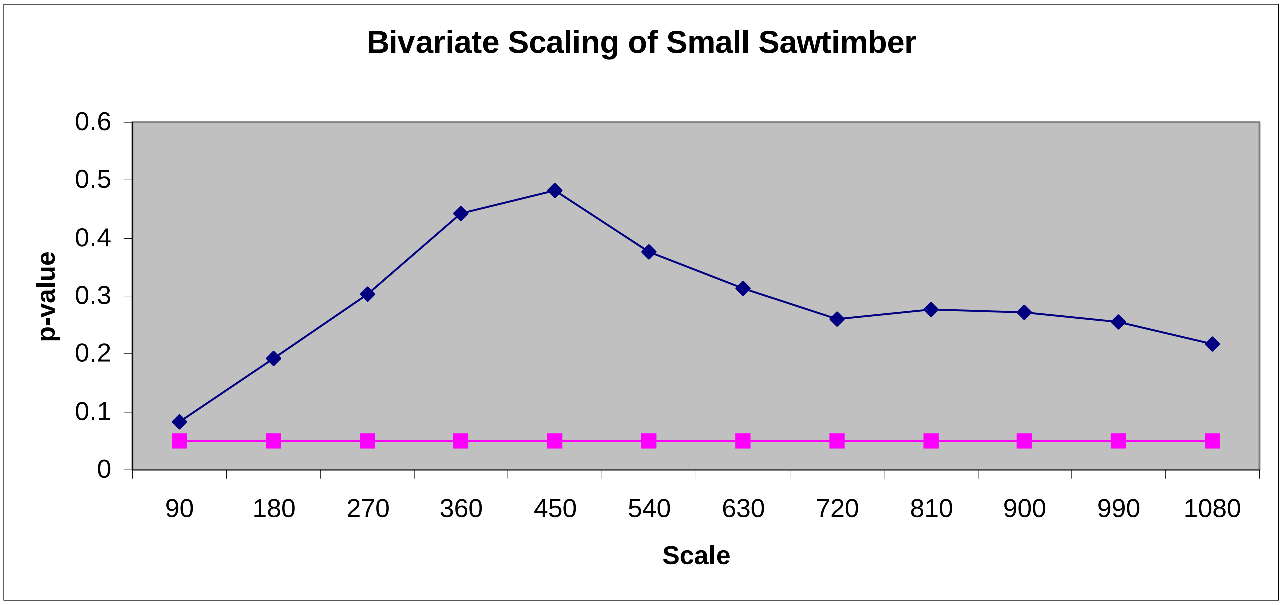

Figure 4: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Small sawtimber at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

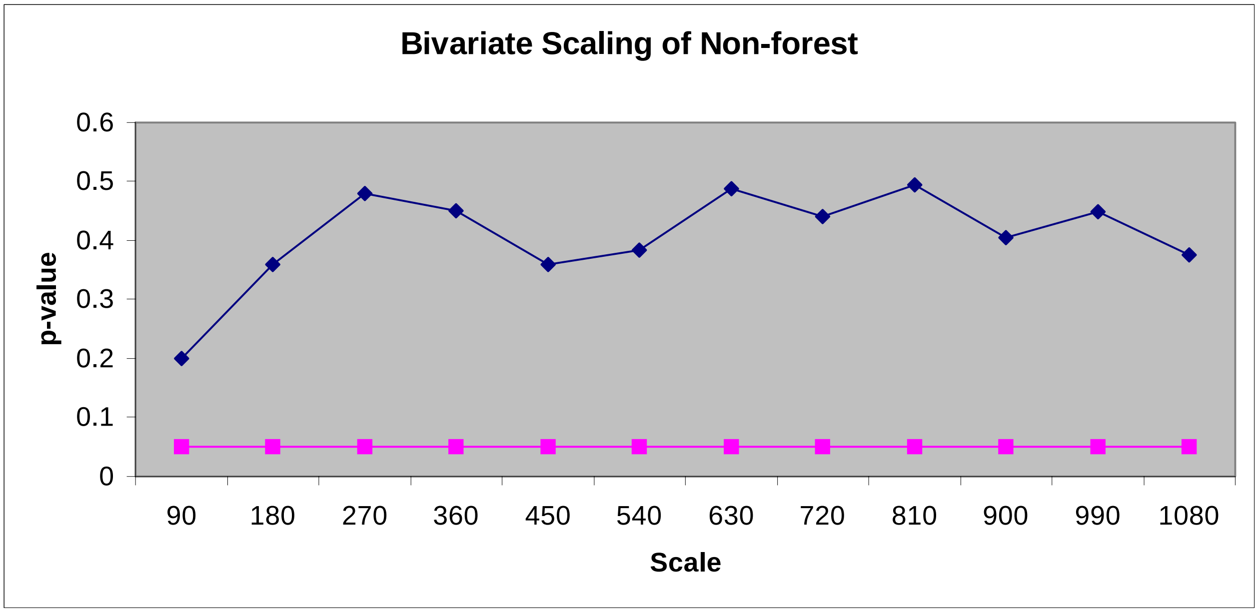

Figure 5: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Non-forest at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used (p<0.05).

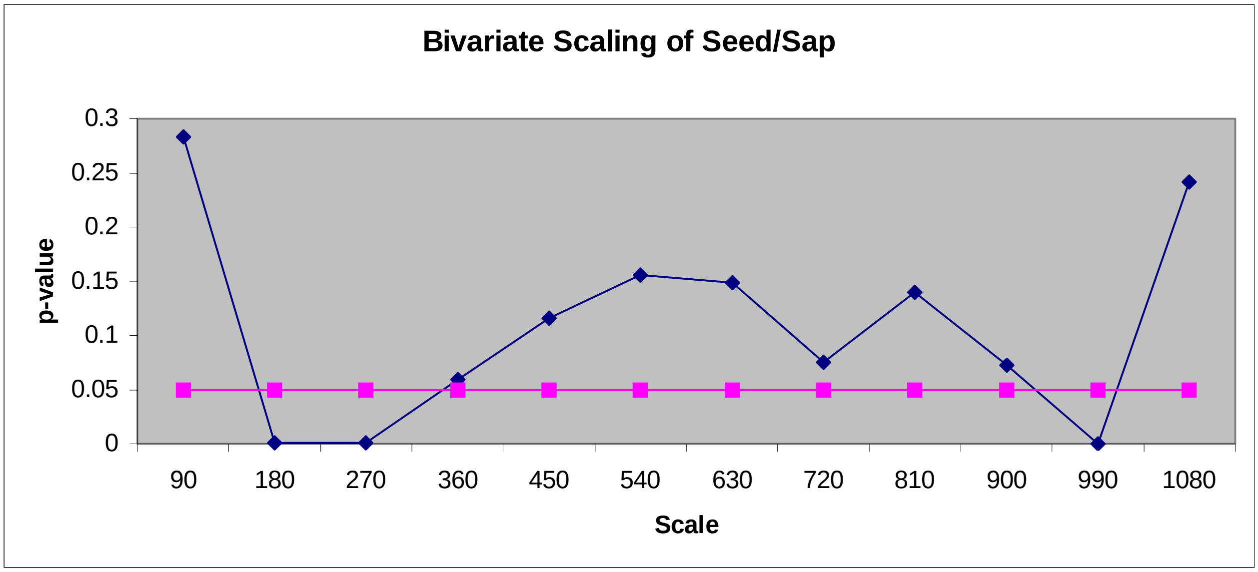

Figure 6: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Seedling/Sapling timber at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used (p<0.05).

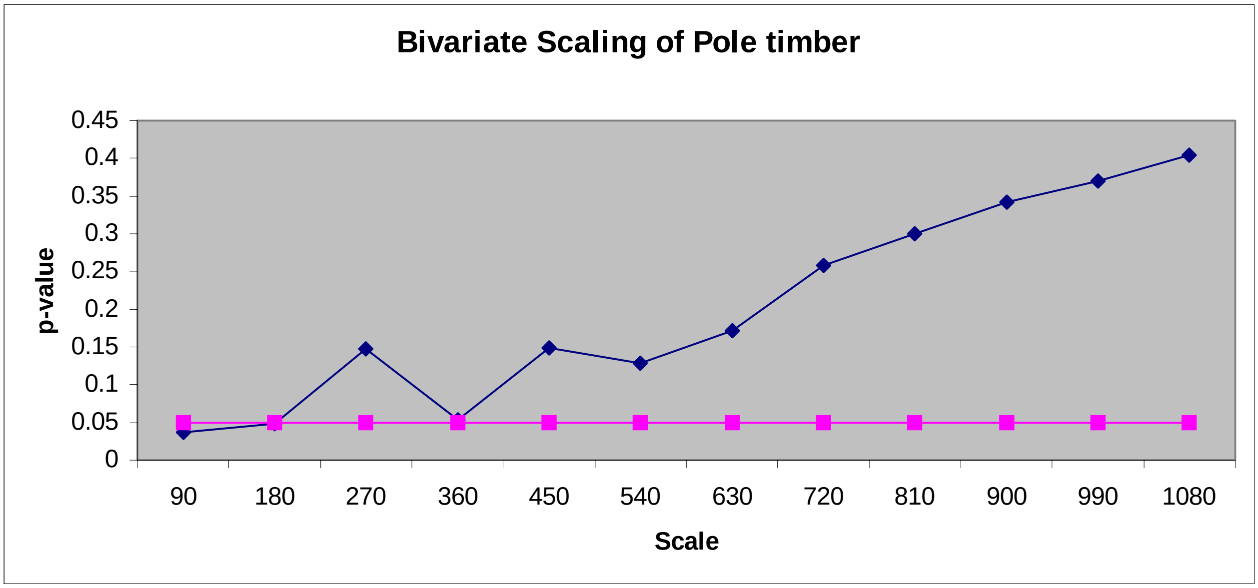

Figure 7: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Pole timber at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used (p<0.05).

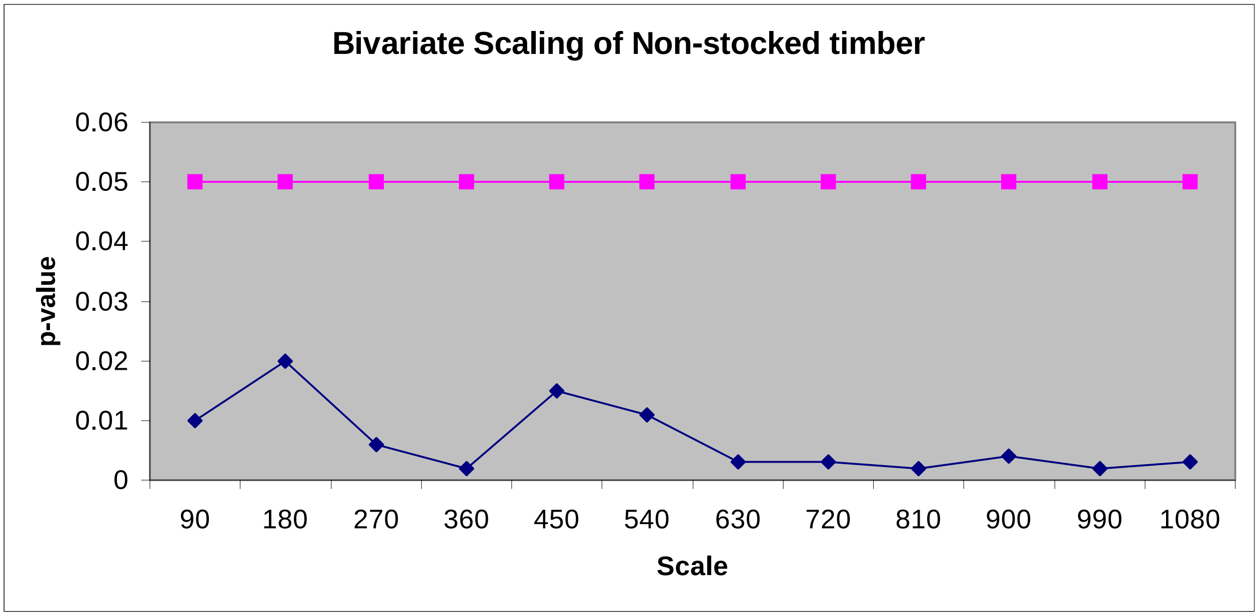

Figure 8: Results of bivariate scaling coupled with FRAGSTATS class metric Percentage of Landscape (PLand) of Non-stocked timber at scales 90m-1080m . Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used (p<0.05).

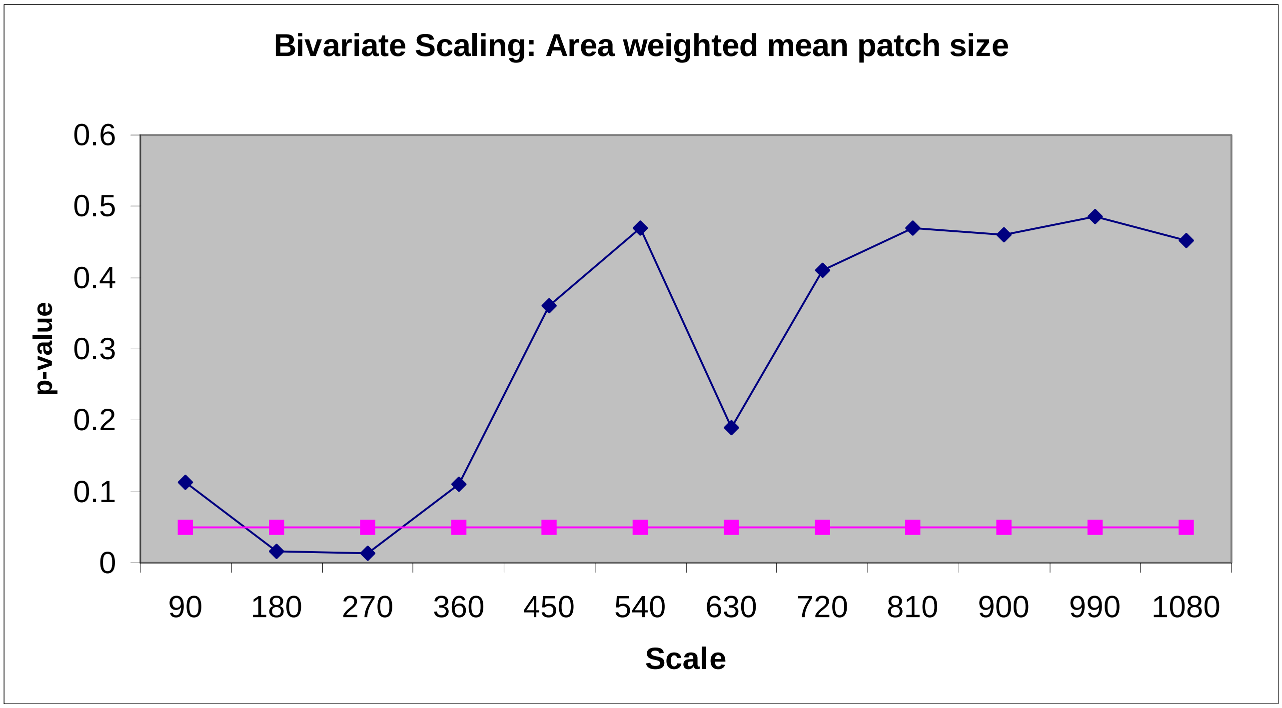

Figure 9: Results of bivariate scaling coupled with FRAGSTATS landscape metric Area Weighted Mean Patch Size (AREA_AM) at scales 90m-1080m . Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

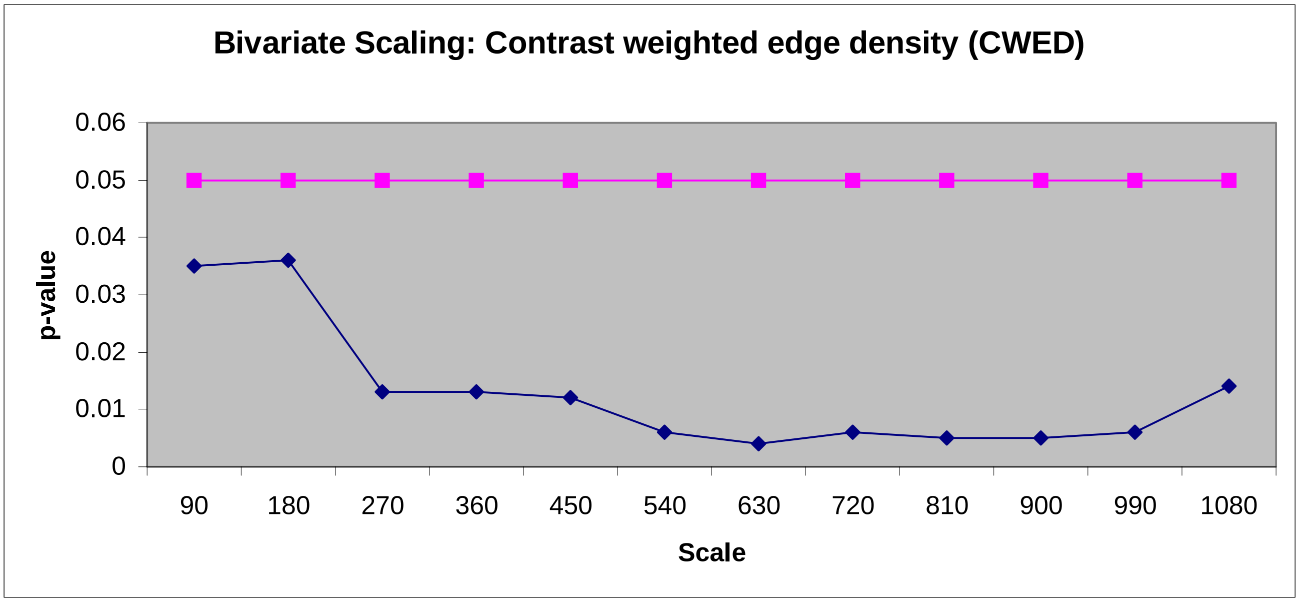

Figure 10: Results of bivariate scaling coupled with FRAGSTATS landscape metric Contrast Weighted Edge Density (CWED) at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

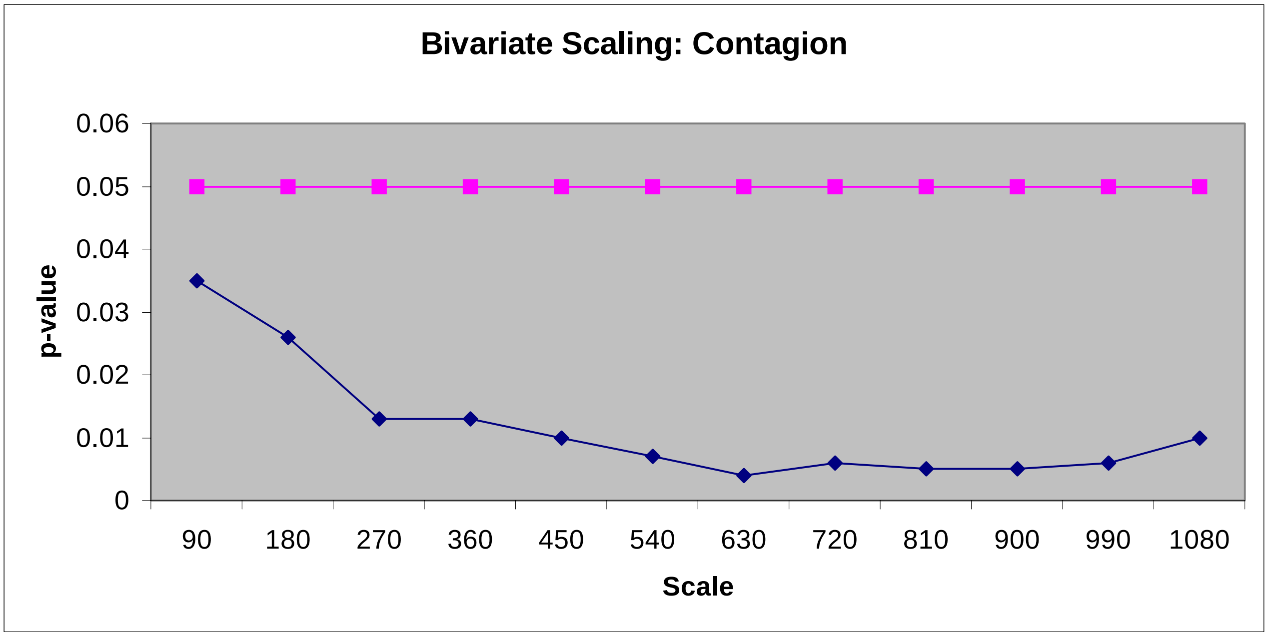

Figure 11: Results of bivariate scaling coupled with FRAGSTATS landscape metric Contagion at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

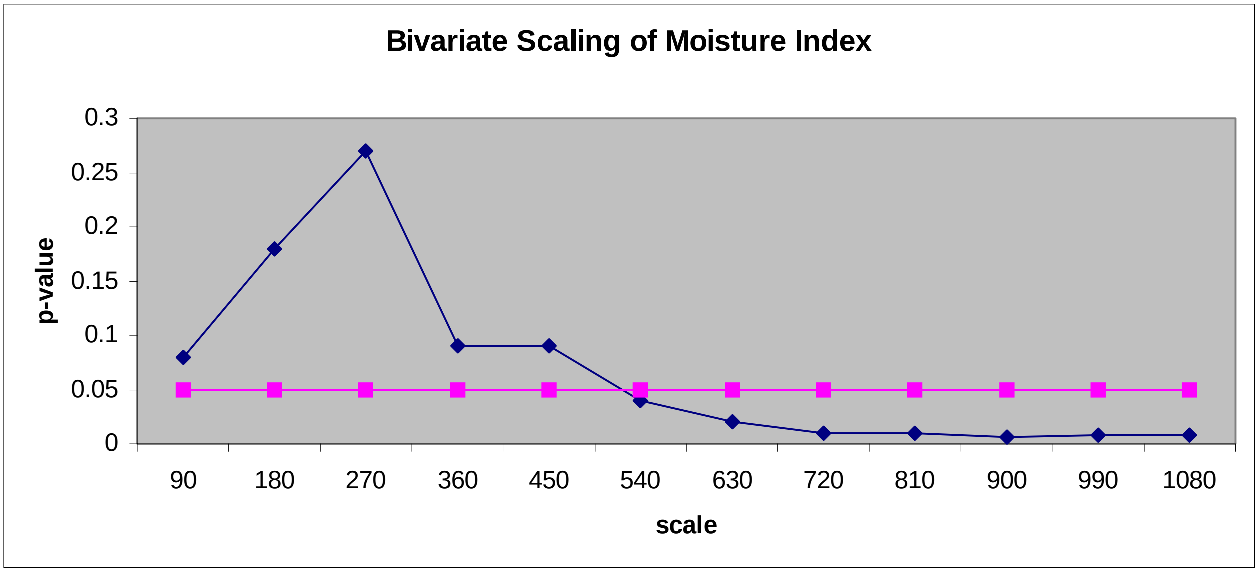

Figure 12: Bivariate scaling of Moisture Index at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

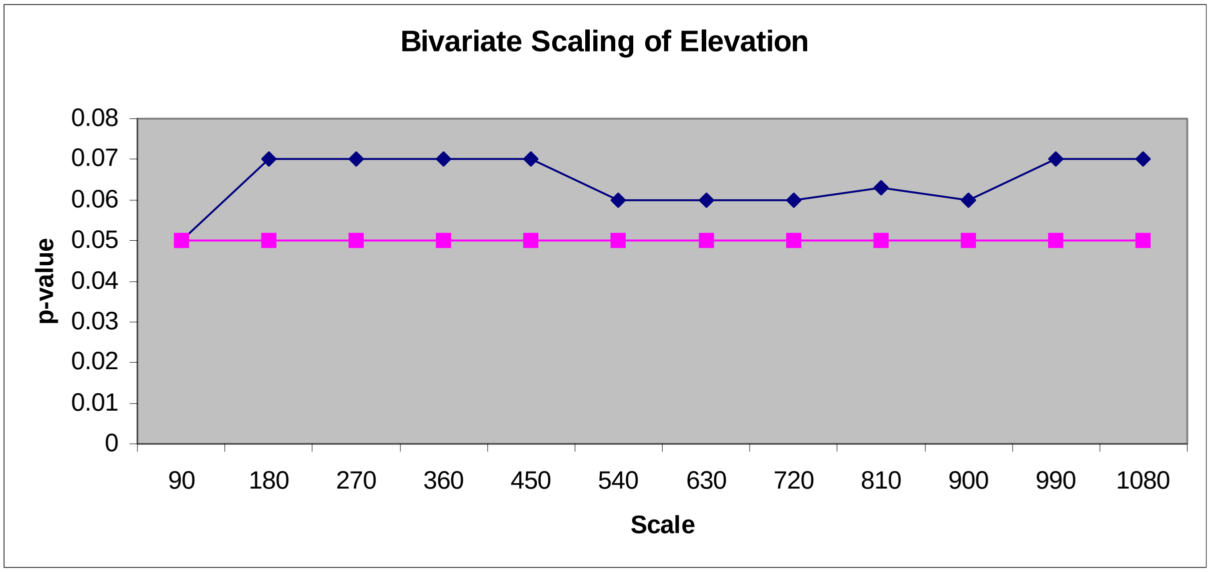

Figure 13: Bivariate scaling of Elevation at scales 90m-1080m. Blue line denotes results from individual Wilcoxon Rank Sum tests. Pink line denotes significance level used ($p<0.05$).

Chapter Two:

Landscape Genetics of *Martes americana* in northern Idaho

INTRODUCTION

Landscape Genetics

Habitat composition and configuration are important factors influencing dispersal patterns, and population persistence and growth. Ultimately these processes influence genetic diversity. Yet quantifying the relationship between landscape patterns and biological processes can be difficult. Habitat fragmentation leads to a decrease in landscape connectivity, thus hindering movement among resource patches (Taylor et al. 1993). Barriers are perceived uniquely by each individual species, and in ways that may not correspond to our accustomed assumptions of connectivity (Weins 2001). Heterogeneity caused by fragmentation can create movement barriers since less favorable habitat may not provide cover against predators or distances between remnant patches may be greater than those that a species is able to cross effectively (Arnold et al. 1993). In response, movement and dispersal of individuals may be altered by landscape fragmentation. This alteration can have dramatic consequences on populations due to: 1) reduction in gene flow between populations, leading to a loss of genetic diversity within fragments (Coulon et al. 2004; Frankham et al. 2002); 2) alteration of source/sink dynamics; or 3) recolonization of habitat following local extinction events. Dispersal and number of migrants between populations are important factors in population persistence, genetic structure and diversity, and species distribution.

Traditional species presence and movement studies such as radio-telemetry and mark-recapture analyses aim to quantify relationships between survival, dispersal distances, and ecological conditions. These studies are well suited for incorporation in large-scale manipulative landscape configuration experiments that measure organism movement and survival rates in response to fragmentation (McGarigal and Cushman 2002). However, mark-recapture studies are often extremely expensive to implement, take years to produce reliable results, and generally do not provide large landscape-level sample sizes. Likewise, telemetry studies are often limited in spatial scope, sample size and pseudoreplication (Cushman 2006; Litvaitis et al. 1994).

Alternatively, molecular genetic techniques can circumvent these problems by providing large samples of individual genotypes distributed across very large geographical areas. Expense is often minimized by using cost-effective, non-invasive sampling methods. This ability to produce very large sample sizes cost-effectively across large study areas makes landscape genetics one of the most powerful approaches currently available to study the influences of spatial pattern in resources and environmental conditions on organism distribution, movement, and gene flow (Cushman 2006, Cushman et al. 2006). The field of landscape genetics is a relatively young science aimed at quantifying evolutionary processes such as gene flow, genetic drift, and selection through the fusion of landscape ecology and population biology (Manel et al. 2003). It has emerged out of recent improvements in molecular genetic tools and an array of powerful spatial analysis methods and Geographic Information Systems (GIS), and allows researchers to correlate genetic patterns with landscape and environmental features (Manel et al. 2003).

Genetic data can be used to quantify movement of individuals, dispersal, immigration and emigration, and the effects of landscape pattern change on metapopulation dynamics (Holderegger and Wagner 2006). Indirect approaches such as genetic analyses have proved very useful in estimating population level parameters, and can be computed across different geographical scales. This field has greatly improved our understanding of how geographical and environmental features structure genetic variation at both the population and individual levels, and can provide information concerning the interaction between landscape features and micro-evolutionary processes. Ultimately, understanding landscape effects on genetic connectivity provides insight into population connectivity, identifying functional corridors, and species distribution.

Individual vs. Population Level Analyses

Traditionally, most population genetic studies use models that assume populations are discretely bounded, isolated and internally panmictic (Cushman et al. 2006). In order to assess genetic differences among defined populations and subpopulations, F statistics and assignment tests are often used (Mills and Allendorf 1996; Wright 1943). Most conventional approaches are based on assignment of individuals to populations using methods that maximize within-group genetic similarity, or sample groups of the focal species and calculate F_{ST} between populations. Many existing computer programs, such as STRUCTURE (Pritchard et al. 2000), will cluster individuals into discrete subpopulations and perform analyses. Subsequently, researchers often perform post hoc analyses in which they attempt to identify potential causes of the observed population structure.

There are several technical and logical limitations to these "cluster-and-explain" approaches (Cushman et al. 2006). First, there is often substantial internal structure within populations (Van Horn et al. 2004; Wright 1943) and it is often difficult to define discrete boundaries between populations. In vagile species, it is more common for populations to be either distributed in low densities between high-density "populations" or to be continuously distributed (Cushman et al. 2006; Manel et al. 2003). Second, these clustering approaches are designed to identify discrete groups, and will do so even if there are actually none. This leads to large risks of erroneously identifying discrete structure when gradient-type genetic patterns are functions of distance or landscape resistance. Third, the post-hoc effort to associate putative "groups" with environmental features runs a very high risk of obtaining incorrect results, and provides no rigorous framework to compare multiple alternative hypotheses of the factors that drive genetic structure. Classical population genetic analyses consist of sampling groups of individuals from predefined populations, and then estimating allele frequencies and parameters, such as genetic distance and *F*-statistics (Nei 1987; Weir & Cockerham 1984). For more continuously distributed populations, individuals are at risk of being grouped on the basis of somewhat arbitrarily criteria, such as morphological differences, geographical distance, or political boundaries (Manel et al. 2007; Pritchard *et al*. 2000).

An alternative to the population-level approach is to use the individual as the unit of observation. Spatial genetic patterns can be assessed at an individual level without defining populations in advance. This is extremely valuable, as it provides a means to evaluate the degree of support for discretely bounded populations versus alternative models in which genetic structure is related to the distance or movement cost between individuals. Many individual based approaches use spatially referenced individual genotypes, and can reveal genetic patterns and identify migrants without prior assumptions about population boundaries. Individual-based approaches can be applied across a wider range of geographical scales, from within local populations to the continental level, and to any organism showing genetic variation (Manel et al. 2007). The scale at which landscape variables have the greatest influence on gene flow is important to identify processes influencing species biology (Storfer et al. 2007).

In this study, I used landscape genetic techniques to describe genetic sub-structure within the *Martes americana* population in northern Idaho and correlate these genetic patterns with environmental features, such as barriers and mountain ranges, and to understand how landscape features structure populations. Individuals were sampled across the study landscape, genetic relatedness between individuals was determined, and their genetic structure was correlated with specific landscape and environmental features (Coulon et al. 2004; Cushman et al. 2006; Manel et al. 2003).

American marten (*Martes americana*) are habitat specialists that depend on mature and old growth forest types in the western United States (Ruggiero et al. 1994). Marten populations are sensitive to forest fragmentation (Bissonette et al. 199; Hargis 1996) and the spatial configuration of patches of remnant mature forest is an important component of their environment (Chapin et al. 1998). Changes in land management practices and forest fragmentation can have a dramatic effect on landscape connectivity and dispersal of animals, potentially reducing gene flow within populations (Coulon et al. 2004).

Objectives

In this study, I used molecular genetic data gathered from *Martes americana* to quantify genetic continuity of this population in the Idaho Panhandle National Forest (IPNF) in northern Idaho. In order to identify patterns and processes influencing genetic continuity of *Martes americana* within the IPNF, I used both a spatial genetics data set and a landscape structure data set. Using the genetics data set, I employed an individual based approach to calculate pairwise genetic distances between individual animals. In this case each individual marten is the unit of observation and populations are not defined *a priori*. Landscape data includes structural and compositional components that quantify the quality of habitat as well as the surrounding matrix. Focusing on processes that drive landscape connectivity and quality rather than just spatial patterns alone will give insight into the genetic patterns of this marten population.

Three Alternative Organizational Models

I used molecular genetic data to test three mutually exclusive organizational models (Figure 1) concerning the effects of landscape composition on movements of *Martes americana* within my study area of the Idaho Panhandle National Forest (IPNF) in northern Idaho (Figure 2). I used genetic data coupled with landscape mapping of multiple environmental attributes to identify spatial genetic structure in my study region without having to *a priori* identify discrete populations. I tested organizational models (Cushman et al. 2006) concerning genetic structure of *Martes americana* in the IPNF. The three organizational models that I tested are Isolation by Distance, Isolation by Barrier, and Isolation as a function of Landscape Resistance.

Identifying barriers to gene flow is a major strength of the landscape genetics approach. Barriers can be defined as physical features such as roads, valleys, rivers etc., or environmental features such as temperature and moisture gradients. Epps et al. (2005) demonstrated that genetic diversity and structure in desert bighorn sheep (*Ovis canadensis nelsoni*) was negatively correlated with fenced highways, encroaching human development, and waterways. In my study I identified three potential barriers to the movement of martens that potentially may divide the regional population into three discrete, non-overlapping subpopulations. These barriers are 1) the Kootenai River trench between Bonners Ferry and the Canadian Border 2) the Kootenai River valley upstream of Bonners Ferry to the Montana Border, and 3) the Naples Valley south of Bonners Ferry to Sandpoint (Figure 2). These three potential barriers separate the Selkirk, Purcell and Cabinet Mountains and this organizational model represents a single hypothesis in which the marten population is subdivided into three discrete subpopulations, one population in each of these mountain ranges.

Isolation by distance is the second organizational model I tested. In continuous populations with limited dispersal rates, levels of gene flow tend to decrease with increasing geographic distances, which in turn will result in increasing genetic differentiation among individuals. This process is referred to as Isolation By Distance (IBD) (Wright 1943), and is a spatial pattern that can be determined by analyzing the distribution of pairwise estimates of genetic distances between individuals relative to the pairwise geographic distances between individuals (Rousset 2000). A model of IBD is based on Wright's neighborhood size assuming genetic equilibrium (equilibrium between genetic variability introduced by mutations and gene flow lost through genetic drift at each generation: Rousset Chapt. 4, 2004), and also assumes that the relationship between genetic and geographic distances can allow estimates of dispersal distances if density is known (Hardy 2003; Rousset 2000). This model assumes that individuals disperse equally in all directions. Taking landscape and environmental features into account, the effect of landscape features such as topography could cause a departure from IBD, as found by Coulon et al. 2004 and Cushman et al. 2006.

Isolation by landscape resistance gradients is the third organizational model I tested. In contrast to the Isolation by Barriers and Isolation by Distance organizational models, in Isolation by Landscape Resistance I specified a number of separate hypotheses (See full description below) which describe potential joint effects of multiple landscape features, such as elevation, canopy closure, seral stage, and roads on the genetic structure of the population. My goal was to determine the relative support for isolation by distance and isolation by barriers in comparison with models of isolation by landscape resistance, and if isolation by landscape resistance proved to be the best organizational model, a sub-goal is to identify the specific combination of landscape variables and their operative scales which are most strongly related to observed patterns of genetic substructure in this marten population.

METHODS

Genetic Sampling

Genetic samples were collected using non-invasive hair snare techniques in the Idaho Panhandle National Forest between 2003-2006. These methods are outlined in Chapter 1 (See *Genetic Methods*).

Genetic Analyses

Identification of individual martens was determined using nuclear DNA following methods outlined in Schwartz et al. 2006. For this analysis, I used genetic samples from *Martes americana* obtained over three sampling years of 2003-04, 2004-05, and 2005-06. Samples were analyzed at the Wildlife Genetics Lab within the U.S.F.S. Rocky Mountain Research Station in Missoula, MT. One hair sample per hair-snare station was analyzed to obtain a successful genotype. If the first sample failed, and one or more additional hair samples for that particular station remained, processing continued until a successful genotype was obtained. This resulted in a maximum of one marten genotype for each geographic location. If more than one animal is detected at a single site, one individual was chosen at random to represent that geographic location. Hair samples were extracted using Qiagen DNeary Tissue kit (Qiagen Inc., Hilden, Germany) with modifications as outlined in Mills et al. (2001). Marten samples were identified using primers previously used on marten. Marten samples were genotyped at 7 variable microsatellite loci (Table 1). Deviations from Hardy-Weinberg proportions, heterozygote excess and deficiency were analyzed with program GENEPOP (Version 3.1d; Raymond and Rousset 1995). Genetic variability for each locus within a population was estimated by calculating the mean number of alleles (A), observed heterozygosity (Ho), expected heterozygosity (He), and allelic richness. Probability of identity (Evett and Weir 1998) was calculated. In order to estimate gene flow between the Selkirk, Purcell, and Cabinet mountain ranges, global F_{st} and F_{st} by mountain range was calculated with program FSTAT 2.9.3. F_{st} is a measure of genetic divergence among subpopulations that ranges from 0-1. A measure closer to 0 would represent a subpopulation with equal allele frequencies, while a measure closer to 1 would imply subpopulations are completely different (Allendorf and Luikart 2007). A Principle Components Analysis (PCA) was performed using genetic data of all samples to look for population substructure based on location within the study area. Data were organized by mountain range (Selkirk, Purcell, or Cabinet) to look for any obvious substructure.

Genetic Distance

Martens detected at sample sites were assumed to be representative of the population of martens at that site. For each individual marten, alleles from a seven locus genotype were coded as 0 (allele absent), 1 (heterozygous for that allele), or 2 (homozygous for that allele). This resulted in a matrix with 51 columns, one for each allele in the sampled population, and 70 rows, one for each individual marten detected. A dissimilarity matrix was calculated on all pairs of sampled martens using the Bray-Curtis percentage dissimilarity measure among individuals (Cushman et al. 2006; Legendre and Legendre 1998).

Isolation by Geographic Distance

To test the hypothesis of Isolation By Distance (IBD), I used Euclidean distance between all pairs of martens in the landscape. This hypothesis predicts that genetic similarity will decrease with increasing geographic (Euclidean) distance. I generated a cost matrix based on the Euclidean distances between all pairs of martens based on UTM coordinates at the points of marten detections. This IBD model assumes that Euclidean distance between individuals is the only factor that influences genetic differences. If this hypothesis is true, then all other hypotheses concerning genetic structure of marten populations within the IPNF must be false. Using partial Mantel tests, this hypothesis assumes that there will be no barrier or landscape resistance effects independent of Euclidean distance (Table 2).

Isolation by Barrier

There are three mountain ranges within my study landscape, which are the Selkirk, Purcell, and Cabinet mountains. The Selkirk mountain range lies to the west of the Kootenai River Valley, while the Purcell mountain range lies east of this valley, and the Cabinet mountains are directly below this (Figure 2). I used a categorical model matrix that predicts panmixia within each mountain range (Selkirk, Purcell, and Cabinet), but not between all three mountain ranges. This model of isolation by barrier assumes that the valleys between each mountain range are barriers to gene flow separating three internally panmictic subpopulations. If this hypothesis is true, then the alternative hypotheses of isolation by distance or landscape resistance gradients must be false.

Using partial Mantel tests, this hypothesis assumes that there will be no distance or landscape resistance effects independent of isolation by barrier (Table 2).

Isolation by Landscape Resistance

A priori, I identified a number of landscape and environmental features that could have a measurable effect on population structure of American marten in the IPNF based on previously published marten studies (Bissonnette et al. 1997; Buskirk and Powell 1994; Hargis et al.1999; Phillips et al. 1994; Taylor 1993). My sub-hypotheses are both study-area specific as well as marten specific hypotheses developed to test landscape factors that structure marten populations within the IPNF. In order to test specific hypotheses regarding landscape features, I created resistance surfaces that assign resistance to movement values to each cell across the landscape based on different landscape attributes. Factors that promote or impede movement of animals can be formalized into resistance surfaces (e.g. Cushman et al. 2006). Each of these resistance surfaces represents an alternative hypothesis regarding factors that may impede or promote marten movement across the landscape.

I developed landscape resistance surfaces based on four factors that have previously been reported to influence habitat selection by American martens: elevation, roads, seral stage based on Diameter and Breast Height (DBH) (Table 3), and Percent Canopy cover (1-100%). Percent canopy cover was taken from National Landcover Data (NLCD) and clipped to encompass my study area only. The DBH layer was taken from the U.S. Forest Service Region 1 Vegetation Mapping project and clipped to cover my study area. The roads map was produced by a related project in the same study area

(Sloan et al. pers com.) and contains all roads in the study area, divided among three types: highways, paved roads and unpaved forest roads. The elevation variables were derived from a 30m DEM (USGS 2000). All of these base maps were resampled to 30m pixel size.

Landscape-Resistance Modeling

Quantifying the relationship between landscape structure and gene flow can give biologists insight into connectivity of populations and metapopulations through space and time. Examining correlations between genetic similarity of individuals across large landscapes and hypothetical movement cost models can yield reliable inferences about population connectivity. By linking these least cost models to the actual patterns of genetic similarity among individuals it is possible to obtain comprehensive evidence describing the relationship between landscape structure and gene flow, and to produce species-specific maps of landscape connectivity. Least cost paths are also valuable in identifying landscape variables that facilitate gene flow and function as corridors, thus linking individuals (Spear et al. 2005; Vignieri 2005).

Calculating Least Cost Distances among Marten Locations for Each Hypothesis

I computed the cumulative cost distances of traversing the least-cost route from each individual marten to every other marten's location for each landscape resistance hypothesis. This calculation is essentially the path of movement an individual would likely take in order to avoid inhospitable areas and facilitate ease of movement. I used the COSTDISTANCE function in ArcGIS (ESRI 2003) to create cost matrices of the least-cost distance from each marten to every other marten detected within the landscape across all of the resistance surfaces.

The cost matrices for the isolation by distance and isolation by barrier model are described below. From each resistance surface for the single-variable of elevation, canopy closure and DBH, I derived a matrix of movement costs based upon the least-cost movement paths between pairs of individuals. I then compared the genetic distance among individuals with the cost of movement paths between them and identified the functions at which each factor had the strongest relationship with marten genetic structure. Once these significant functions were identified I created the multiple-variable resistance surfaces described in Table 5.

Scaling Landscape Factors

A priori, I wanted to determine the functional relationship at which each landscape feature is most strongly correlated with marten genetic structure. Therefore, I produced a range of functionally scaled resistance surfaces for each of DBH, Canopy Cover, and Elevation. I produced eight functionally scaled resistance surfaces for canopy cover and DBH by transforming the base layers with power functions to determine the functional relationship. Forest type classification using DBH and percent canopy cover and were evaluated over eight different levels that included linear and power functions of 0.2, 0.4, 0.6, 0.8, 2nd, 3rd, and 4th power (Figures 3 and 4). As seen in Figures 3 and 4, landscape resistance predicted by these power functions ranges from strongly convex to strongly concave over the range of the x-variable. Using a scaling method by fitting functions to each resistance factor, I can identify the scaling function at which each factor is most important in predicting marten genetic structure across my study landscape in the Idaho Panhandle National Forest (IPNF). Both percent canopy cover and DBH raster maps were rescaled to 1-10, 1 being lowest resistance and 10 being highest resistance.

Elevation serves as a proxy for climate (e.g. snowpack) and vegetation composition. Landscape resistance due to elevation was modeled as a Gaussian function, on the expectation that marten should show a unimodal optimum in movement ability with respect to elevation. Transforming elevation using a Gaussian function results in the delineation of an optimum elevation for marten movement. This optimum elevation delineates the highest habitat quality/lowest resistance, with habitat quality declining and landscape resistance increasing at elevations above and below this optimum. The form of the Gaussian function is defined on the basis of the optimum elevation and the standard deviation. The standard deviation defines the rate of change in landscape resistance above and below the optimum. The optimum elevation is assigned a minimum resistance of 1 and the maximum resistance of 10. I decided to evaluate marten response to a range of possible optimum elevations and a range of potential standard deviations of the Gaussian resistance function in order to find the combination of elevation and standard deviation to which marten genetic patterns are most strongly related. I tested elevation resistance grids with elevation optima ranging from 1,200m to 2,000m and standard deviations around the optima ranging from 300m to 1000m in 100m increments. In all, there were 9 levels of elevation (1,200m-2,000m) and 8 levels of standard deviation (300m-1,000m in 100m increments), giving a factorial combination of 72 elevation/standard deviation models (Table 4).

One level of roads was considered and represented as a categorical function. Roads were classified as either a major highway or “other road”. Other roads included county and U.S. Forest Service roads that were both gated and un-gated. This Roads factor was scaled 1-10, 1 being low resistance and 10 being high resistance. All non-road pixels were given a value of 1, major highways a resistance of 10, and other roads resistance of 5.

Resistance of each factor to gene flow was calculated across 72 functions of elevation, one level of roads, eight functions of forest type classes and eight functions of percent canopy cover. All four factors are scaled from 1 (low resistance) to 10 (high resistance). This allows a range of functions representing each factor permitting the relative importance of each factor to be tested. After completing Mantel and Partial Mantel tests and evaluating Mantel’s r correlation coefficient and most significant Monte-Carlo p-value, the best function for each factor was chosen to be included in multi-variable landscape resistance models.

Multi-variable Landscape Resistance Hypotheses

Multivariate resistance surfaces were composed containing the factorial combinations of the best function of each of the four factors. In each test, genetic distance is the response variable and each resistance hypothesis is a predictor variable (Table 5). Resistance grids corresponding to each factor were combined into models by addition. These hypotheses were represented by GIS raster maps where the cell values were equal to the proposed resistance value of each cell to gene flow. After addition, the minimum value on the combined raster maps was 4, which is the sum of the minimum values of the 4 factors, and the maximum resistance to gene flow could be 40. Resistance grids were created for each hypothesis tested.

Support for Models of Genetic Structure

These landscape models are hypotheses in which the cumulative cost of movement across a resistance surface is the best predictor of genetic structure for *Martes americana* in the Idaho Panhandle National Forest. The three organizational models are logically mutually exclusive. The isolation by barrier model hypothesizes that genetic structure is broken into three disjunct and internally panmictic subpopulations. If this model is true then isolation by distance and isolation by landscape resistance must be false. Conversely, the isolation by distance model hypothesizes that genetic differences are a function of only the geographical distance between individuals. If this model is true then the barrier and the landscape resistance models must be false. Likewise, if isolation by landscape resistance is the correct hypothesis, then there will be no distance or barrier effects independent of isolation by landscape resistance.

I used Mantel (Mantel 1967) and partial Mantel tests (Legendre et al. 2002; Smouse et al. 1986) to assess the support for each of my hypotheses. The Mantel test evaluates the correlation between two dissimilarity matrices. It is essentially a multivariate distance regression in which the dependent variables are a matrix of genetic dissimilarity and the independent variables are a matrix of cost distances among pairs of sample locations. These dissimilarity matrices may represent the pair-wise differences among sample units based on one or many variables. In my case, the dependent variable matrix reports the percentage dissimilarity in 51 alleles across seven micro-satellite loci, and the independent variable matrices reflect pair-wise cost distance among the locations at which each individual marten was sampled for each resistance hypothesis.

A significant Mantel correlation would indicate that the genetic differences among individual martens are correlated with the resistance hypothesis represented in the independent variable matrix. Values of pair-wise distance matrices, such as those used in Mantel tests, are not independent; changing the position of one observation would change n-1 of the distances. Therefore, significance tests are obtained through Monte Carlo permutation, in which the rows and columns of one of the matrices are shuffled and the test statistic recalculated after each permutation. The probability of the null hypothesis being correct given the data is the proportion of permutations that lead to a higher correlation coefficient. I used 10,000 permutations for each hypothesis tested. As they are correlation coefficients, Mantel and partial Mantel coefficients can also be used to evaluate support. Higher values of the Mantel correlation coefficient (r) statistic indicate greater support for a particular landscape resistance hypothesis.

While the Mantel test only allows a comparison between two distance matrices, a Partial Mantel test can be used to compare three or more matrices. The partial Mantel test tests the correlation between two distance matrices after removing, or partialling out, the influences of a third matrix. Simply put, this a comparison between two dissimilarity matrices while controlling for the third. In the partial Mantel test, to calculate the relationship between dissimilarity matrices A and B, while partialling out the effects of matrix C, the test statistic is calculated by constructing a matrix of residuals, A’, of the regression between A and C, and a matrix of residuals, B’, of the regression between B and C. The two residual matrices, A’ and B’, are then compared by a standard Mantel test. The test of statistical significance is also done through randomization tests. Rows and columns of one of the matrices are randomly permuted many times, with the correlation recalculated each time.

In order to determine which of the three organizational models was most supported by the data, I used causal modeling on resemblance matrices (Cushman et al. 2006; Legendre 1993; Legendre and Troussellier 1988). Causal modeling on resemblance matrices uses a series of partial Mantel tests to evaluate the pattern of support for alternative causal explanations for an observed pattern of genetic relatedness. Each alternative model will have a diagnostic set of expected outcomes in a series of partial Mantel tests, which provides a decisive means to reject unsupported alternative hypotheses and determine which of the remaining hypotheses receive the greatest support. In each test, genetic distance is the response variable and each resistance hypothesis is a predictor variable. Partial Mantel correlation coefficients are used to weigh the degree of support of each hypothesis and determine causality (Legendre and Troussellier 1988). Each of the three alternative models (Isolation by Barriers, Isolation by Distance, Isolation by Landscape Resistance) can be falsified with causal modeling by comparing the results of a set of diagnostic partial Mantel tests to the expected significance pattern for each (Table 6).

RESULTS

Genetic Results

Martens were detected at 152 stations over the three sampling years of 2003-04, 2004-05, and 2005-06. Genotypes for 90 stations (59.2%) were obtained, and 70 unique individual marten were detected. Within 7 variable microsatellite loci the number of alleles ranged from 5-10 alleles per loci, with a total of 51 alleles. Overall, observed heterozygosity was less than expected heterozygosity in 6 out of 7 loci (Table 1). Global Fst was 0.045, and pairwise Fst was 0.016 between Purcell and Cabinet mountain ranges, 0.033 between Purcell and Selkirk mountain ranges, and 0.025 between the Cabinet and Selkirk mountain ranges (Table 7). These results demonstrate a low degree of differentiation among marten populations in the Idaho Panhandle National Forest. Results from the PCA using location data shows little substructure within the sampled population of *Martes americana* (Figure 5).

Isolation by Distance Model

Genetic distance was significantly correlated with Geographic (Euclidean) distance using the model G ~ D (r =0.1723, p=0.0001). This relationship was not significant when the partial Mantel test G ~ D | B was performed (r =0.0527, p=0.085), controlling for the effect of a barrier (Table 8).

Isolation by Barrier Model

Genetic distance was significantly correlated with mountain range as a barrier

Using the model G ~ B (r =0.1764, p=0.0001). This relationship was significant when the partial Mantel test G ~ B | D was performed (r =0.0652, p=0.0393), controlling for the effect of Euclidean distance (Table 8).

Landscape Resistance Models

Resistance of each factor to gene flow was initially evaluated in a univariate fashion across 72 levels of elevation (Table 9), one level of roads scaled from 1 (low resistance) to 10 (high resistance), eight functions of forest type classes and 8 functions of percent canopy cover. For each factor, the best function was chosen to be included in the multivariate landscape resistance model after completing Mantel and Partial Mantel tests and evaluating Mantel's r and most significant Monte-Carlo p-value. These hypotheses were represented by GIS raster maps where the cell values were equal to the proposed resistance value of each cell to gene flow. Resistance surfaces were composed containing the factorial combinations of each of these four factors. After addition, the minimum value on the combined raster maps was 4, which is the sum of the minimum values of the 4 factors. Resistance grids were created for each hypothesis tested.

A) Elevation

Each landscape resistance model tested was based on pairwise least cost paths between individual martens and ranked by Mantel's r and Monte-Carlo p-value. Out of 72 models of landscape resistance with respect to elevation, Elevation 1600m with a standard deviation of 600m (r = 0.2019, p=0.0001) was the most supported elevation model based on both Monte-Carlo p-value and Mantel's r value (Table 9) correlated to marten genetic structure within the study landscape, and was also supported when Euclidean distance (r =0.12022, p=0.0007) was partialled out, and mountain range as a barrier (r = 0.0999, p=0.0132) was partialled out (Table 11). Therefore, Elevation 1600m with a standard deviation of 600m was included in the full factorial of landscape resistance models as the elevation factor.

B) DBH and Canopy Cover

Eight functions of DBH forest classification, eight functions of percent canopy cover, and one level of roads were modeled with respect to genetic distance, geographic (Euclidean) distance, and mountain range as a barrier. The highest ranked DBH and Canopy Cover variables were DBH 2nd, Percent Canopy Cover Linear, and Roads (Table 10). Partial Mantel tests for all four variables are shown in Table 11. These three variables were then used to model a full factorial combination of these factors.

C) Factorial Models

The full factorial combination included the highest ranked variables of DBH 2nd, Percent Canopy Cover Linear, Elevation 1600m with a standard deviation of 600m, and Roads. The factorial modeling of these 4 variables yielded a total of 33 landscape resistance hypothesis models based on pairwise least cost paths between all individual martens (Table 12). All models were evaluated first by significance of the Monte-Carlo p-value and then by the largest Mantel's r value. The model G ~ Elevation 1600m with a standard deviation of 600m (r = 0.2019, p=0.0001) was the most highly supported landscape resistance model correlated to genetic structure of *Martes americana* within the Idaho Panhandle National Forest (Table 13). This most supported model of Elevation 1600m s.d. 600m was also significant when geographic distance (r = 0.1202, p = 0.0007) and barrier (r = 0.0999, p=0.0132) was partialled out (Table 11). Models G ~ DBH 2nd (r =0.1828, p=0.0001) and G ~ Canopy Cover Linear (r = 0.1798, p=0.0001) were ranked as the 2nd and 3rd highest ranked models respectively (Table 13). There were no additional significant partial models of the landscape resistance factorial analysis (Table 13).

Based on Monte-Carlo p-value and Mantel's r correlation coefficient, the landscape resistance model depicting the least cost path is the most supported model compared to models of Isolation by Barrier and Isolation by Distance (Euclidean distance) (Table 14). Both alternative models of Isolation by Barriers and Isolation by Distance were falsified with causal modeling by comparing the results of a set of diagnostic partial Mantel tests to the expected significance pattern for each hypothesis (Table 15).

DISCUSSION

In this study, non-invasively collected hair samples produced genetic data used to model genetic relationships of *Martes americana* in the Idaho Panhandle National Forest (IPNF). Genetic data was paired with empirical landscape structure data and GIS layers to correlate genetic structure with landscape and environmental features. This analytical approach provides insight on how geographical and environmental features structure genetic variation at both the population and individual levels, and is important in quantifying factors acting upon gene flow.

Local genetic structure in *Martes americana* was examined using global and pairwise F_{st} coefficients, however no robust global genetic structure or strong structure based on mountain range was apparent from the F_{st} coefficients (Table 7). These results demonstrate a low degree of differentiation among marten populations in the Idaho Panhandle National Forest, demonstrating that animals within this study area are not a discrete finite population or group of subpopulations, but conversely a large continuously distributed population. A low level of genetic structure among individuals and all samples is frequent in a highly mobile species such as American marten. Some marten populations have been documented to be separated by large distances of several hundred kilometers or more and appear genetically undifferentiated (Kyle and Strobeck 2003), indicating a weak genetic structure. This low level of structure within this population in the IPNF may be in part attributed to high levels of gene flow within the study region. F-statistics are widely used in population genetic studies but may not always be a good measure of spatial genetic structure within populations and a priori defining populations could lead to incorrect conclusions.

A total of 164 models of genetic structure were tested. I tested landscape genetic relationships of *Martes americana* against Geographical (Euclidean) Distance, large valleys as Barriers, and 160 hypotheses of Landscape Resistance. Genetic distance was based on pairwise genetic distance between individuals and was significantly correlated with geographical (Euclidean) distance, however this relationship was not significant when mountain range as a Barrier was partialled out. Genetic distance was tested against mountain range as a Barrier, and I found this model significant both by itself and when Geographical Distance was partialled out (Table 8). I tested hypotheses of landscape resistance to gene flow based on DBH size classes, Percent Canopy Cover, Roads, and Elevation. Fitting functions to factors revealed that DBH 2^{nd}, % Canopy Cover Linear, Elevation 1600m with a standard deviation of 600m, and Roads were the most significant variables based on Mantel's r and Monte-Carlo p-value. Factorial combinations of these 4 variables were tested (Table 13).

In my study landscape within the Idaho Panhandle National Forest in northern Idaho, the genetic distance between individual American martens was most highly correlated ($r = 0.2019$, $p=0.0001$) with a Gaussian function on elevation with a minimum resistance of 1600m, standard deviation of 600m (Table 13, Figure 7). This relationship was significant when both mountain range as a barrier and geographic distance were partialled out (Table 11). Although there were 14 other significant landscape resistance models, G ~ Elevation 1600 std.dev. 600m had the highest ranked Mantel's r value and was much higher than the 2^{nd} and 3^{rd} models respectively. In this study, the roads variable was not a particularly strong ($r=0.1353$, $P=0.001$) barrier to gene flow in American marten.

Although the Mantel's r correlation coefficients in this study were generally low, Coulon et al. (2004) state that when working at the individual level there is high inherent variability when compared to interpopulation analyses, and it is an inherent characteristic to obtain lower correlation coefficients using individual-based approaches. It is worth noting that the Mantel's r values reported in this study are substantially higher than most previously published values (e.g. Broquet et al. 2006; Coulon et al. 2004; and Cushman et al. 2006), indicating a relatively substantial degree of genetic differentiation along landscape resistance gradients. For example, Cushman et al. (2006) conducted a similar analysis within the same study area in northern Idaho using black bears (*Ursus americana*). Mantel's r values ranged from 0.1257 (highest) to 0.0477 (lowest), and were substantially lower than those in my study (Cushman et al. 2006, unpublished data). A study by Broquet et al. 2006 on *Martes americana* in northwestern Ontario, Canada focused on models of IBD and landscape connectivity, and contained Mantel r-values that were nearly an order of magnitude lower than Mantel r-values in my study. And finally, Coulon et al. (2004) used Mantel and partial Mantel tests to hypotheses of IBD and least-cost paths for European roe deer (*Capreolus capreolus*) in southwestern France. Mantel's r-values for all hypotheses they tested ranged from –0.0001 (males) to 0.031 (females), and remained very low comparatively.

Several landscape genetics studies tested only one or very few models of landscape resistance against isolation by distance, global models of mating, or barriers (Andreassen et al. 1998; Coulon et al. 2004; Coulon et al. 2006; Danielson and Hubbard 2000). Most other publications using hypothesis testing don't evaluate a large number of landscape resistance hypotheses and therefore don't have a large number of significant models. Therefore, after ranking models by most significant Monte-Carlo p-value I relied on evaluating models by highest Mantel's r correlation coefficients. My study used a multi-model approach to test multiple hypotheses concerning landscape resistance to identify environmental factors that appear to drive landscape genetic patterns in American marten.

Martens are responding significantly to elevation, which corresponds to specific levels of snow cover and forest types appearing at these elevations. In the IPNF, precipitation ranges from a mean of more than 1,778 mm in the highest peaks to less than 762.0 mm within the rain shadow of the Selkirk Mountains. Heavy snow cover in this study region excludes predators (e.g. *Canis latrans*), and provides high-quality hunting conditions via subnivean space. By avoiding lower elevations, genetic structure of *Martes americana* is tightly correlated with connectivity at mid to high elevations. Forest types at this elevation are within the subalpine zone characterized by moist, cool sites where Subalpine fir (*Abies lasiocarpa)* and Engelmann spruce (*Picea engelmannii)* are codominant above 1300m, and a diverse mixed forest of Western Larch (*Larix occidentalis*), Western White pine (*Pinus monticola*), and Spruce-fir mix are the dominant species. My results suggest that the genetic structure of martens is determined by the connectivity of stands of mature spruce-fir mixed forest at mid to high elevations. Dispersal distances of juveniles may be shorter due to high quality habitat areas at these elevations, thus robustly structuring genetic relationships within this landscape.

Comparing multiple hypotheses concerning geographic distance, barrier, and landscape resistance allowed me to examine the importance of evaluating multiple working hypotheses. Hypotheses of isolation by geographic distance and valleys between mountain ranges as a barrier were not found to be the most highly supported drivers of genetic structure of *Martes americana*. I was able to evaluate and rank 160 landscape hypotheses and find the most highly supported model correlated to marten genetic structure in the Idaho Panhandle National Forest. If I had just tested models of geographic distance or isolation by barrier, I would have spuriously concluded that a model of Isolation by barrier was in fact the primary driver of genetic structure in *Martes americana* in the Idaho Panhandle National Forest. Many molecular and population biology studies stop when a model of IBD is supported (e.g. Broquet et al. 2006), and may in fact miss the true drivers of genetic structure if landscape resistance models are not tested. My model of landscape resistance was a much stronger driver genetic structure than other models of geographic distance and barrier (Table 14). In this study, the hypothesis of isolation by barrier was not supported as a driver gene flow for *Martes americana* in the Idaho Panhandle National Forest when landscape resistance was partialled out. The model of isolation by geographic distance was not significant when barrier was partialled out, therefore it is not a supported hypothesis (Table 15). Least cost modeling is a valuable tool in identifying landscape variables that facilitate gene flow and functional movement corridors. Biologists and managers are able to work towards facilitating movement corridors that maximize quality habitat that facilitates gene flow (Vignieri 2005). Exploring the processes that cause genetic patterns and identifying areas of genetic discontinuity are important tools for species conservation.

CONCLUSION

Indirect approaches based on genetic structure are valuable and useful in determining mechanisms such as dispersal, immigration and emigration rates, genetic drift, and the effects of landscape and environmental features. Landscape genetics modeling allowed me to test explicit hypotheses concerning genetic structure of *Martes americana* in the Idaho Panhandle National Forest. I evaluated multiple competing models to infer causation using pairwise genetic distance between individuals rather than between previously defined groups or populations. Spatially explicit data was used to model factors acting upon gene flow. In this study, it was important to test a range of alternative and falsifiable explanations to identify the true driver of genetic structure across the landscape. Comparing models of Isolation by distance, Isolation by barrier, and landscape resistance hypotheses allowed me to falsify distance and barrier, and rank alternative landscape resistance hypotheses. It was highly important to test a range of landscape hypotheses that included factors most important to gene flow, and that were at the proper scale. These results will help managers to identify biologically important corridors that facilitate movement and gene flow within this marten population.

Genetic structure can have a substantial time lag associated with changes in gene flow. Genetic structure results from both historic and contemporary processes, and current observed genetic structure may be more representative of processes that occurred as a result of a previous landscape pattern or configuration (Cushman et al. 2006; Storfer et al. 2007). This lag time can be attributed to effective population size (N_e) and population substructure (Wright 1943). It is important to consider time lag to equilibrium number of generations it takes to reach equilibrium. In addition, *Martes americana* in the IPNF are considered a fur bearing species and are currently trapped throughout my study area, which could cause concerns about detection rates and allelic richness.

CHAPTER 2: TABLES

Table 1: Summary of genetic diversity of 7 microsatellite loci of a *Martes americana* population in Northern Idaho. Allelic richness (*A*) and expected heterozygosity (*He*), and (*Fis)* are shown.

Locus	# of alleles	*A*	*Ho*	*He*	*Fis*
Ma8	8		0.750	0.762	0.016
Gg7	10		0.652	0.807	0.191
Ggu234	5		0.539	0.560	0.037
Ggu216	8		0.701	0.771	0.090
Gg3	6		0.626	0.634	0.013
Ma1	9		0.573	0.763	0.249
Ma2	5		0.747	0.721	-0.036

Table 2: Models of genetic distance by geographic distance and genetic distance by barrier. Mantel tests and partial Mantel tests were used in landscape genetics modeling testing the hypotheses of Isolation by barrier and Isolation by distance. G = Genetic Distance, D = Geographic Distance, and B = Barrier.

Model	**Test**
G ~ D	Mantel Test
G ~ B	Mantel Tests
G ~ D | B	Partial Mantel Test
G ~ B | D	Partial Mantel Test

Table 3: Forest Class Type based on Diameter at Breast Height and timber classification on both state and federal lands in the Idaho Panhandle Nat'l Forest used as a resistance map in landscape resistance modeling. Diameter at Breast Height (DBH) is presented.

	Class	Description
1	Large Sawtimber	Dominant and codominant trees with DBH > 16 in
2	Small Sawtimber	Dominant and codominant tress with DBH 8-16 in
3	Pole Sawtimber	Dominant and codominant trees with DBH 3-7.9 in
4	Seedling/Sapling	Crop trees< 4.5 ft and < 3 in DBH (open canopy)
5	Non-forest	Non-forested areas

Table 4: Models of elevation and standard deviations tested to predict genetic structure of *Martes americana* with respect to landscape resistance. A factorial combination of all elevations and all standard deviations was used, yielding 72 total elevation models. The highest ranked elevation model was then used in factorial landscape resistance modeling.

	Elevation Ranges (m)	Standard deviations (m)
1.	1200	300
2.	1300	400
3.	1400	500
4.	1500	600
5.	1600	700
6.	1700	800
7.	1800	900
8.	1900	1000
9.	2000	------

Table 5: Models of Landscape Resistance hypothesized to have an effect on genetic structure of *Martes americana* in the IPNF. Models include1 level of Roads, 8 Percent Canopy Cover power functions, and 8 DBH power functions. Models were tested using Mantel and Partial Mantel's tests. Highest ranked models were then used in the full factorial modeling. G = Genetic Distance.

	Model	**Test**
1	G ~ DBH L	Mantel
2	G ~ DBH 2nd	Mantel
3	G ~ DBH 3rd	Mantel
4	G ~ DBH 4th	Mantel
5	G ~ DBH 0.2	Mantel
6	G ~ DBH 0.4	Mantel
7	G ~ DBH 0.6	Mantel
8	G ~ DBH 0.8	Mantel
9	G ~ Canopy L	Mantel
10	G ~ Canopy 2nd	Mantel
11	G ~ Canopy 3rd	Mantel
12	G ~ Canopy 4th	Mantel
13	G ~ Canopy 0.2	Mantel
14	G ~ Canopy 0.4	Mantel
16	G ~ Canopy 0.6	Mantel
17	G ~ Canopy 0.8	Mantel
18	G ~ Roads	Mantel
19	G ~ DBH L | Barrier	Partial Mantel
20	G ~ DBH L | Euclidean	Partial Mantel
21	G ~ DBH 2nd | Barrier	Partial Mantel
22	G ~ DBH 2nd | Euclidean	Partial Mantel
23	G ~ DBH 3rd | Barrier	Partial Mantel
24	G ~ DBH 3rd | Euclidean	Partial Mantel
25	G ~ DBH 4th | Barrier	Partial Mantel
26	G ~ DBH 4th | Euclidean	Partial Mantel
27	G ~ DBH 0.2 | Barrier	Partial Mantel
28	G ~ DBH 0.2 | Euclidean	Partial Mantel
29	G ~ DBH 0.4 | Barrier	Partial Mantel
30	G ~ DBH 0.4 | Euclidean	Partial Mantel
31	G ~ DBH 0.6 | Barrier	Partial Mantel

32	G ~ DBH 0.6 | Euclidean	Partial Mantel
33	G ~ DBH 0.8 | Barrier	Partial Mantel
34	G ~ DBH 0.8 | Euclidean	Partial Mantel
35	G ~ Canopy L | Barrier	Partial Mantel
36	G ~ Canopy L | Euclidean	Partial Mantel
37	G ~ Canopy 2nd | Barrier	Partial Mantel
38	G ~ Canopy 2nd | Euclidean	Partial Mantel
39	G ~ Canopy 3rd | Barrier	Partial Mantel
40	G ~ Canopy 3rd | Euclidean	Partial Mantel
41	G ~ Canopy 4th | Barrier	Partial Mantel
42	G ~ Canopy 4th | Euclidean	Partial Mantel
43	G ~ Canopy 0.2 | Barrier	Partial Mantel
44	G ~ Canopy 0.2 | Euclidean	Partial Mantel
45	G ~ Canopy 0.4 | Barrier	Partial Mantel
46	G ~ Canopy 0.4 | Euclidean	Partial Mantel
47	G ~ Canopy 0.6 | Barrier	Partial Mantel
48	G ~ Canopy 0.6 | Euclidean	Partial Mantel
49	G ~ Canopy 0.8 | Barrier	Partial Mantel
50	G ~ Canopy 0.8 | Euclidean	Partial Mantel
51	G ~ Roads | Barrier	Partial Mantel
52	G ~ Roads | Euclidean	Partial Mantel
53	G ~ DBH 2nd | Canopy L	Partial Mantel
54	G ~ Canopy L | DBH 2nd	Partial Mantel

DBH = Diameter at Breast Height, Canopy = Percent Canopy Cover, L=Linear, 2nd, 3rd, 4th, 0.2, 0.4, 0.6 are power functions, Barrier = Mountain range as a barrier, and Euclidean = Euclidean Distance.

Table 6. Causal modeling and diagnostic expectations for partial Mantel tests that allow for the rejection of incorrect causal explanations of genetic patterns. G = matrix of pair-wise genetic dissimilarity; B = model matrix separating individuals among the three mountain ranges; D = matrix of pair-wise Euclidean distance among sampled individuals; L = matrix of pair-wise cost distance among sampled individuals for a landscape resistance hypothesis. G ~ B indicates a Mantel test between genetic dissimilarity and the Barrier model matrix; G ~ B|D indicates a partial Mantel test between genetic dissimilarity and the Barrier model matrix, while partialling out the effects of Euclidean distance among sampled individuals.

Hypothesis	**Expected Significant Positive Correlations**	**Expected to be Non-significant**
Barrier	G ~ B G ~ B| D G ~ B| L	G ~ L| B G ~ D| B
Geographic Distance	G ~ D G ~ D| B G ~ D| L	G ~ L| D G ~ B| D
Landscape Resistance	G ~ L G ~ L| D G ~ L| B	G ~ B| L G ~ D| L

Table 7: Pairwise F_{ST} (measure of genetic divergence) of *Martes americana* population genetic data by mountain range in the IPNF.

Purcell	Cabinet	Selkirk	
0.000	-------	--------	Purcell
0.016	0.000	--------	Cabinet
0.033	0.025	0.000	Selkirk

Table 8: Results of models testing the hypotheses of Isolation by barrier and Isolation by distance using Mantel tests and partial Mantel tests. G = Genetic Distance, D = Geographic Distance (Euclidean), and B = Barrier. Mantel's r and corresponding Monte-Carlo p-values are given (significance level based on $p < 0.05$).

Model	**Test**	**Mantel's r**	**p-value**
G ~ D	Mantel Test	0.1723	0.0001
G ~ B	Mantel Tests	0.1764	0.0001
G ~ D | B	Partial Mantel Test	0.0527	0.0850
G ~ B | D	Partial Mantel Test	0.0652	0.0393

Table 9: Results of the factorial elevation and standard deviation models used to predict genetic structure of *Martes americana* with respect to landscape resistance. A factorial combination of all elevations and all s.d.'s were used, yielding 72 total elevation models. The highest ranked elevation model was then used in factorial landscape resistance modeling. Mantel's r and corresponding Monte-Carlo p-values are given (significance level based on p< 0.05).

	Elevation Model	Mantel's r	p-value
1	**G ~ Elev 1600m, s.d. 600m**	**0.201994**	**0.0001**
2	G ~ Elev 1600m, s.d. 500m	0.201848	0.0001
3	G ~ Elev 1200m, s.d. 700m	0.198118	0.0001
4	G ~ Elev 1900m, s.d. 300m	0.188759	0.0001
5	G ~ Elev 2000m, s.d. 300m	0.186804	0.0001
6	G ~ Elev 1800m, s.d. 300m	0.186593	0.0001
7	G ~ Elev 2000m, s.d. 400m	0.183540	0.0001
8	G ~ Elev 1900m, s.d. 400m	0.181351	0.0001
9	G ~ Elev 1700m, s.d. 300m	0.180296	0.0001
10	G ~ Elev 1200m, s.d. 300m	0.178616	0.0001
11	G ~ Elev 2000m, s.d. 500m	0.178377	0.0001
12	G ~ Elev 1800m, s.d. 400m	0.177807	0.0001
13	G ~ Elev 1900m, s.d. 500m	0.175972	0.0001
14	G ~ Elev 1200m, s.d. 500m	0.175854	0.0001
15	G ~ Elev 1200m, s.d. 400m	0.175022	0.0001
16	G ~ Elev 2000m, s.d. 1000m	0.174632	0.0001
17	G ~ Elev 1900m, s.d. 1000m	0.174630	0.0001
18	G ~ Elev 1600m, s.d. 1000m	0.174549	0.0001
19	G ~ Elev 1800m, s.d. 1000m	0.174530	0.0001
20	G ~ Elev 1700m, s.d. 1000m	0.174296	0.0001
21	G ~ Elev 2000m, s.d. 900m	0.174262	0.0001
22	G ~ Elev 2000m, s.d. 700m	0.174196	0.0001
23	G ~ Elev 1900m, s.d. 900m	0.174061	0.0001
24	G ~ Elev 1800m, s.d. 900m	0.174037	0.0001
25	G ~ Elev 2000m, s.d. 800m	0.173984	0.0001
26	G ~ Elev 1600m, s.d. 900m	0.173919	0.0001
27	G ~ Elev 1900m, s.d. 600m	0.173907	0.0001
28	G ~ Elev 2000m, s.d. 600m	0.173907	0.0001
29	G ~ Elev 1900m, s.d. 800m	0.173652	0.0001
30	G ~ Elev 1500m, s.d. 1000m	0.173586	0.0001
31	G ~ Elev 1700m, s.d. 900m	0.173574	0.0001
32	G ~ Elev 1800m, s.d. 500m	0.173381	0.0001
33	G ~ Elev 1800m, s.d. 800m	0.173347	0.0001

34	G ~ Elev 1700m, s.d. 400m	0.173162	0.0001
35	G ~ Elev 1900m, s.d. 700m	0.173116	0.0001
36	G ~ Elev 1600m, s.d. 800m	0.173072	0.0001
37	G ~ Elev 1500m, s.d. 900m	0.172968	0.0001
38	G ~ Elev 1700m, s.d. 800m	0.172856	0.0001
39	G ~ Elev 1800m, s.d. 700m	0.172485	0.0001
40	G ~ Elev 1200m, s.d. 600m	0.172381	0.0001
41	G ~ Elev 1500m, s.d. 800m	0.172123	0.0001
42	G ~ Elev 1800m, s.d. 600m	0.172018	0.0001
43	G ~ Elev 1700m, s.d. 700m	0.171707	0.0001
44	G ~ Elev 1600m, s.d. 700m	0.171702	0.0001
45	G ~ Elev 1500m, s.d. 700m	0.170881	0.0001
46	G ~ Elev 1200m, s.d. 800m	0.170793	0.0001
47	G ~ Elev 1200m, s.d. 900m	0.170462	0.0001
48	G ~ Elev 1200m, s.d. 1000m	0.170311	0.0001
49	G ~ Elev 1700m, s.d. 600m	0.170163	0.0001
50	G ~ Elev 1700m, s.d. 500m	0.170061	0.0001
51	G ~ Elev 1600m, s.d. 300m	0.169243	0.0001
52	G ~ Elev 1500m, s.d. 600m	0.168983	0.0001
53	G ~ Elev 1400m, s.d. 1000m	0.167346	0.0001
54	G ~ Elev 1400m, s.d. 900m	0.167170	0.0001
55	G ~ Elev 1400m, s.d. 800m	0.166890	0.0001
56	G ~ Elev 1300m, s.d. 1000m	0.166809	0.0001
57	G ~ Elev 1300m, s.d. 900m	0.166650	0.0001
58	G ~ Elev 1400m, s.d. 700m	0.166484	0.0001
59	G ~ Elev 1300m, s.d. 800m	0.166399	0.0001
60	G ~ Elev 1300m, s.d. 700m	0.166045	0.0001
61	G ~ Elev 1500m, s.d. 500m	0.165725	0.0001
62	G ~ Elev 1600m, s.d. 400m	0.165671	0.0001
63	G ~ Elev 1400m, s.d. 600m	0.165641	0.0001
64	G ~ Elev 1300m, s.d. 600m	0.165407	0.0001
65	G ~ Elev 1300m, s.d. 500m	0.164063	0.0001
66	G ~ Elev 1400m, s.d. 500m	0.163850	0.0001
67	G ~ Elev 1500m, s.d. 300m	0.161654	0.0001
68	G ~ Elev 1500m, s.d. 400m	0.161045	0.0001
69	G ~ Elev 1400m, s.d. 400m	0.160351	0.0001
70	G ~ Elev 1300m, s.d. 400m	0.159973	0.0001
71	G ~ Elev 1400m, s.d. 300m	0.157814	0.0001
72	G ~ Elev 1300m, s.d. 300m	0.156642	0.0001

Table 10: Mantel test results models of DBH, Percent Canopy Cover, and Roads. Output is shown with Mantel's r and corresponding Monte-Carlo p-values (significance level based on $p < 0.05$). The most supported model is marked by ***. Highest ranked scale of each variable was used for landscape resistance modeling. G = Genetic Distance.

DBH Functions

	Model	Mantel's r	p-value	
1	G ~ DBH L	0.1779644	0.0001	
2	**G ~ DBH 2nd**	**0.1828082**	**0.0001**	***
3	G ~ DBH 3rd	0.1783192	0.0001	
4	G ~ DBH 4th	0.1767269	0.0001	
5	G ~ DBH 0.2	0.1782551	0.0001	
6	G ~ DBH 0.4	0.1756273	0.0001	
7	G ~ DBH 0.6	0.1760266	0.0001	
8	G ~ DBH 0.8	0.1771870	0.0001	

Canopy Functions

	Model	Mantel's r	p-value	
9	**G ~ Canopy L**	**0.1798701**	**0.0001**	***
10	G ~ Canopy 2nd	0.1750581	0.0001	
11	G ~ Canopy 3rd	0.1738078	0.0001	
12	G ~ Canopy 4th	0.1739953	0.0001	
13	G ~ Canopy 0.2	0.1759872	0.0001	
14	G ~ Canopy 0.4	0.1771973	0.0001	
15	G ~ Canopy 0.6	0.1686271	0.0001	
16	G ~ Canopy 0.8	0.1710050	0.0001	

Road Function

17	**G ~ Roads**	**0.1353347**	**0.0001**	***

DBH = Diameter at Breast Height, Canopy = Percent Canopy Cover, L=Linear, 2nd, 3rd, 4th, 0.2, 0.4, 0.6 are power functions, Barrier = Mountain range as a barrier, and Euclidean = Euclidean Distance.

Table 11: Partial Mantel test results of models of DBH, Percent Canopy Cover, Roads, and most highly supported model of Elevation. Output is shown with Mantel's r and corresponding Monte-Carlo p-values (significance level based on $p < 0.05$). G = Genetic Distance.

	Model	Mantel's r	p-value
1	G ~ Elev1600m | Barrier	0.0999138	0.0132
2	G ~ Elev1600m | Euclidean	0.1202238	0.0007
3	G ~ DBH 2nd | Barrier	0.0673110	0.0281
4	G ~ DBH 2nd | Euclidean	0.0665662	0.0288
5	G ~ Canopy L | Barrier	0.0751876	0.0367
6	G ~ Canopy L | Euclidean	0.0524324	0.0949
7	G ~ Roads | Barrier	0.0415319	0.1493
8	G ~ Roads | Euclidean	0.0229962	0.2903

DBH = Diameter at Breast Height, Canopy = Percent Canopy Cover, L=Linear, 2^{nd}, 3^{rd}, 4^{th}, 0.2, 0.4, 0.6 are power functions, Barrier = Mountain range as a barrier, and Euclidean = Euclidean Distance.

Table 12: Factorial Landscape Resistance models used to model the full factorial of resistance to gene flow in *Martes americana*. G = Genetic Distance.

	Model
1	G ~ DBH 2nd
2	G ~ Canopy L
3	G ~ Elev1600m
4	G ~ Roads
5	G ~ DBH 2nd + Roads
6	G ~ DBH 2nd + Canopy L
7	G ~ DBH 2nd + Roads + Elev1600m
8	G ~ Roads + Elev1600m
9	G ~ DBH 2nd + Canopy L + Roads
10	G ~ DBH 2nd + Elev1600m
11	G ~ DBH 2nd + Canopy L + Roads + Elev1600m
12	G ~ Canopy L + DBH 2nd + Elev1600m
13	G ~ Canopy L + Roads
14	G ~ Canopy L + Roads + Elev1600m
15	G ~ Canopy L + Elev1600m
16	G ~ Roads + Elev1600m | Barrier
17	G ~ DBH 2nd + Roads | Barrier
18	G ~ DBH 2nd + Roads + Elev1600m | Barrier
19	G ~ DBH 2nd + Canopy L | Barrier
20	G ~ DBH 2nd + Elev1600 | Barrier
21	G ~ DBH 2nd + Canopy L + Roads | Barrier
22	G ~ Canopy L + DBH 2nd + Elev1600m | Barrier
23	G ~ DBH 2nd + Canopy L + Roads + Elev1600m | Barrier
24	G ~ Canopy L + Roads | Barrier
25	G ~ Canopy L + Roads + Elev1600m | Barrier
26	G ~ Canopy L + Elev1600m | Barrier
27	G ~ DBH 2nd + Roads | Euclidean
28	G ~ DBH 2nd + Canopy L | Euclidean
29	G ~ Roads + Elev1600m | Euclidean
30	G ~ DBH 2nd + Roads + Elev1600m | Euclidean
31	G ~ DBH 2nd + Canopy L + Roads | Euclidean

32	G ~ DBH 2nd + Canopy L + Roads + Elev1600m | Euclidean
33	G ~ DBH 2nd + Elev1600 | Euclidean
34	G ~ Canopy L + DBH 2nd + Elev1600m | Euclidean
35	G ~ Canopy L + Roads | Euclidean
36	G ~ Canopy L + Roads + Elev1600m | Euclidean
37	G ~ Canopy L + Elev1600m | Euclidean

DBH = Diameter at Breast Height, Canopy = Percent Canopy Cover, L=Linear, 2nd, 3rd, 4th, 0.2, 0.4, 0.6 are power functions, Barrier = Mountain range as a barrier, and Euclidean = Euclidean Distance.

Table 13: Results of the factorial landscape resistance models used to model the full factorial of resistance to gene flow in *Martes americana*. Results are ranked by Mantel's r and corresponding Monte-Carlo p-values (significance level based on $p < 0.05$). G = Genetic Distance (Dashed line represents end of 95% confidence interval).

	Model	**Mantel's r**	**p-value**
1	G ~ Elev1600m	0.201994	0.0001
2	G ~ DBH 2nd	0.182808	0.0001
3	G ~ Canopy L	0.179870	0.0001
4	G ~ DBH 2nd + Roads	0.173835	0.0001
5	G ~ DBH 2nd + Canopy L	0.173444	0.0001
6	G ~ DBH 2nd + Roads + Elev1600m	0.172658	0.0001
7	G ~ Roads + Elev1600m	0.172606	0.0001
8	G ~ DBH 2nd + Canopy L + Roads	0.172246	0.0001
9	G ~ DBH 2nd + Elev1600m	0.171844	0.0001
10	G ~ DBH 2nd + Canopy L + Roads + Elev1600m	0.171546	0.0001
11	G ~ Canopy L + DBH2nd + Elev1600m	0.171322	0.0001
12	G ~ Canopy L + Roads	0.170885	0.0001
13	G ~ Canopy L + Roads + Elev1600m	0.170098	0.0001
14	G ~ Canopy L + Elev1600m	0.168918	0.0001
15	G ~ Roads	0.135335	0.0001
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16	G ~ Roads + Elev1600m | Barrier	0.052649	0.09681
17	G ~ DBH 2nd + Roads | Barrier	0.051120	0.10001
18	G ~ DBH 2nd + Roads + Elev1600m | Barrier	0.050853	0.10191
19	G ~ DBH 2nd + Canopy L | Barrier	0.050602	0.10111
20	G ~ DBH 2nd + Elev1600 | Barrier	0.050210	0.10081
21	G ~ DBH 2nd + Canopy L + Roads | Barrier	0.048194	0.11511
22	G ~ Canopy L + DBH 2nd + Elev1600m | Barrier	0.048063	0.11271
23	G ~ DBH 2nd + Canopy L + Roads + Elev1600m | Barrier	0.047981	0.10861
24	G ~ Canopy L + Roads | Barrier	0.046255	0.11761
25	G ~ Canopy L + Roads + Elev1600m | Barrier	0.046062	0.12611
26	G ~ Canopy L + Elev1600m | Barrier	0.04502	0.12781
27	G ~ DBH 2nd + Roads | Euclidean	0.023370	0.24793
28	G ~ DBH 2nd + Canopy L | Euclidean	0.020791	0.25763
29	G ~ Roads + Elev1600m | Euclidean	0.011665	0.31423

30	G ~ DBH 2nd + Roads + Elev1600m | Euclidean	0.010858	0.36404
31	G ~ DBH 2nd + Canopy L + Roads | Euclidean	0.010113	0.37524
32	G ~ DBH 2nd + Canopy L + Roads + Elev1600m | Euclidean	0.000141	0.49325
33	G ~ DBH 2nd + Elev1600 | Euclidean	-0.000233	0.49775
34	G ~ Canopy L + DBH 2nd + Elev1600m | Euclidean	-0.000562	0.51095
35	G ~ Canopy L + Roads | Euclidean	-0.004371	0.54666
36	G ~ Canopy L + Roads + Elev1600m | Euclidean	-0.022499	0.75958
37	G ~ Canopy L + Elev1600m | Euclidean	-0.037270	0.87599

DBH = Diameter at Breast Height, Canopy = Percent Canopy Cover, L=Linear, 2nd, 3rd, 4th, 0.2, 0.4, 0.6 are power functions, Barrier = Mountain range as a barrier, and Euclidean = Euclidean Distance.

Table 14: Correlation between genetic distance and models of landscape resistance, barrier, and geographic distance of *Martes americana* in Northern Idaho. Results are based on 10,000 permutations. Mantel's r and corresponding p-values are given (significance level based on $p < 0.05$).

Model	***Mantel's r***	***Monte-Carlo p-value***
Landscape Resistance	0.20199	0.0001
Barrier	0.1764	0.0001
Distance	0.1723	0.0001

Table 15: Causal modeling and diagnostic expectations results for partial Mantel tests, which allow for the rejection of incorrect causal explanations of genetic patterns. G = matrix of pair-wise genetic dissimilarity; B = model matrix separating individuals among the three mountain ranges; D = matrix of pair-wise Euclidean distance among sampled individuals; L = matrix of pair-wise cost distance among sampled individuals for a landscape resistance hypothesis. G ~ B indicates a Mantel test between genetic dissimilarity and the Barrier model matrix; G ~ B|D indicates a partial Mantel test between genetic dissimilarity and the Barrier model matrix, while partialling out the effects of Euclidean distance among sampled individuals.

Hypothesis	**Expected Significant Positive Correlations**				**Expected Non-significant Correlations**			
		Mantel r	***p-value***			***Mantel r***	***p-value***	
Barrier	G ~ B	0.1764	0.0001	Yes	G ~ L| B	0.0999	0.0132*	No
	G ~ B| D	0.0652	0.0393	Yes	G ~ D| B	0.0527	0.0850	Yes
	G ~ B| L	-0.0016	0.5189*	No				
Geographic Distance	G ~ D	0.1723	0.0001	Yes	G ~ L| D	0.1202	0.0007*	No
	G ~ D| B	0.0527	0.0850*	No	G ~ B| D	0.0652	0.0393*	No
	G ~ D| L	–0.552	0.9211*	No				
Landscape Resistance	G ~ L	0.20199	0.0001	Yes	G ~ B| L	-0.0016	0.5189	Yes
	G ~ L| D	0.12022	0.0007	Yes	G ~ D| L	–0.552	0.9211	Yes
	G ~ L| B	0.0999	0.0132	Yes				

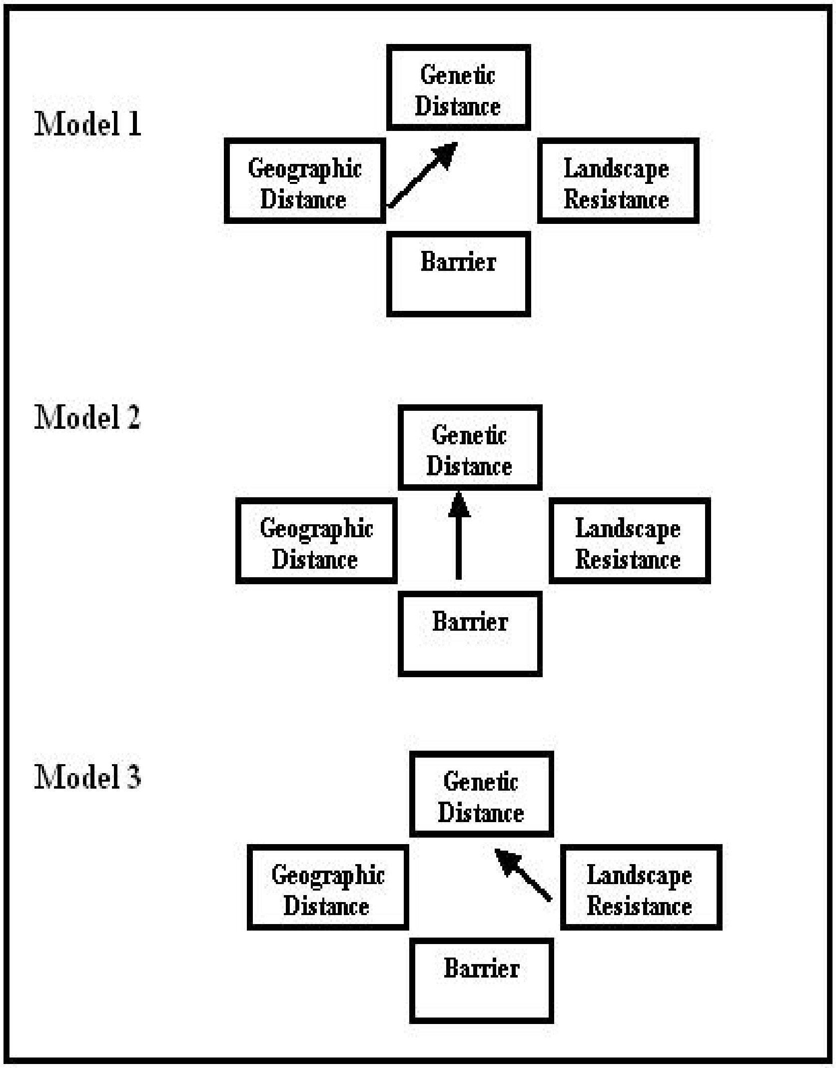

Figure 1: Conceptual models of hypotheses that structure *Martes Americana* populations in the IPNF. Model 1 is Isolation By Geographic Distance, Model 2 is Isolation By Barrier, and Model 3 is Isolation By Landscape Resistance.

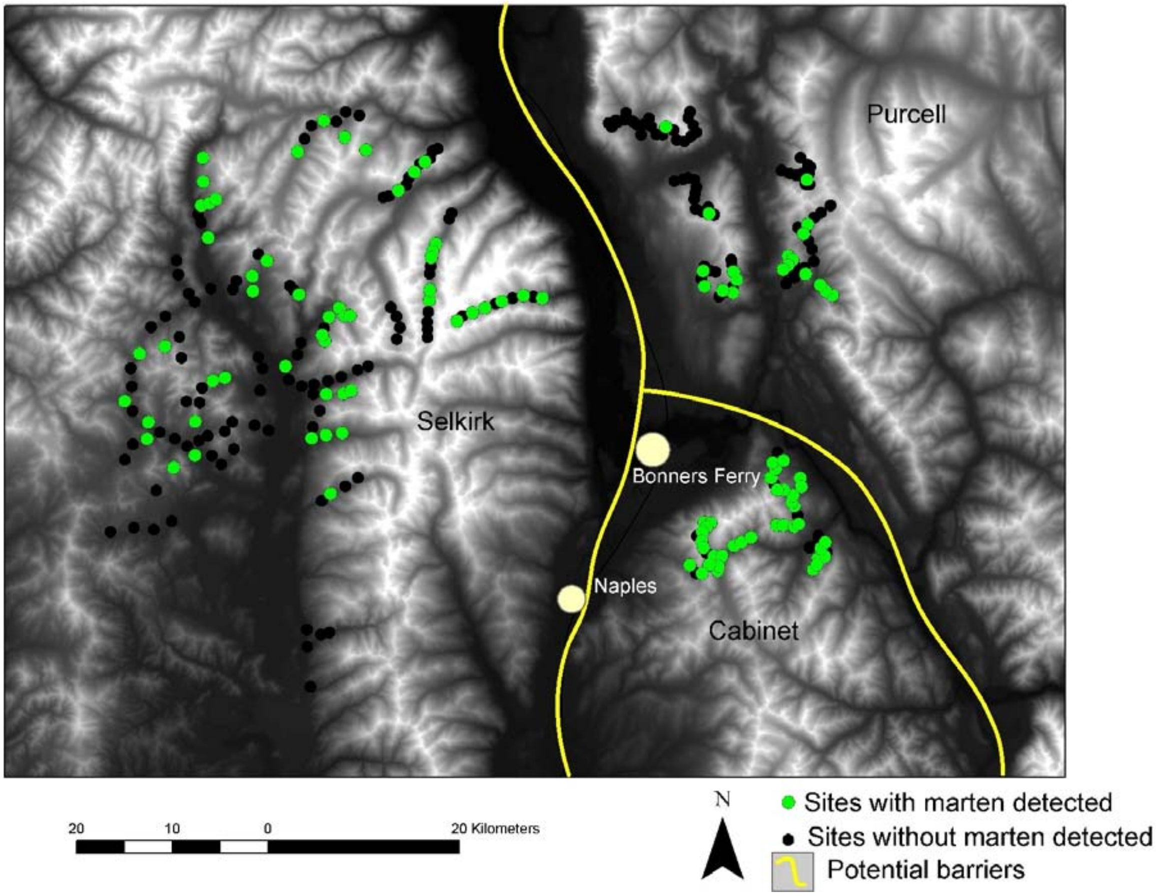

Figure 2: View of study area located in northern Idaho highlighting the spatial location of the Selkirk, Purcell, and Cabinet mountain ranges in relation to each other as well as the Kootenai River Valley. Locations of all survey sites are also shown.

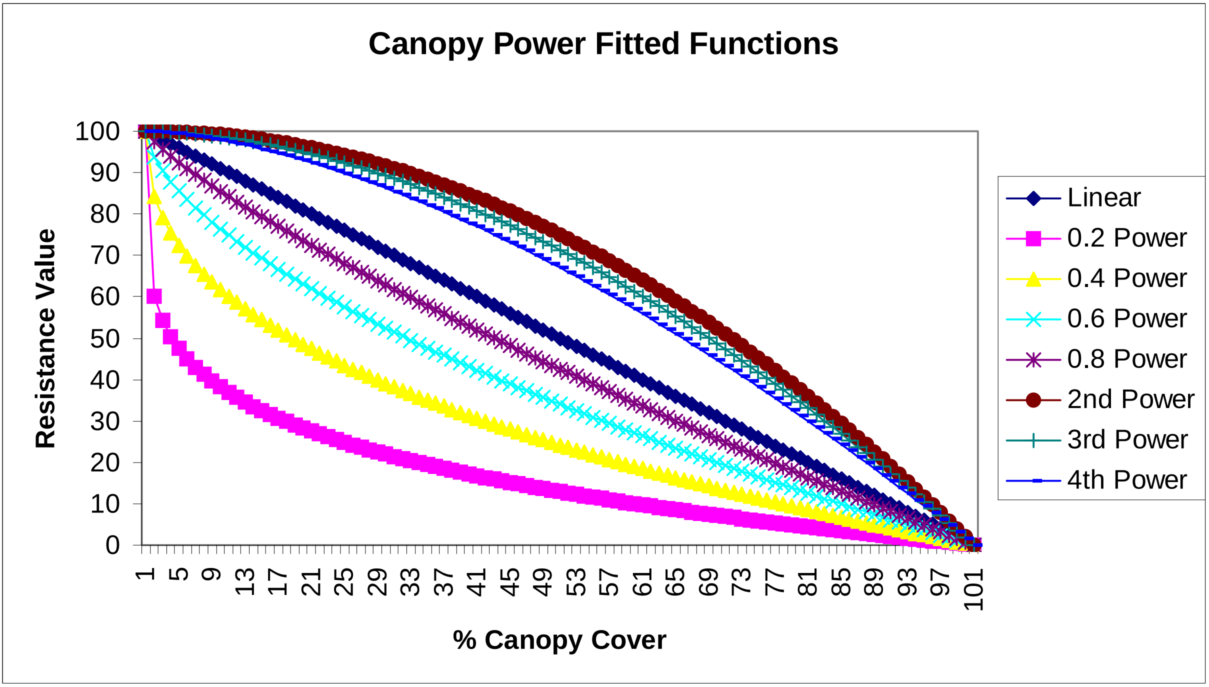

Figure 3: Power fitted functions for percent canopy cover as related to resistance value on the landscape resistance map. Power functions are at 8 different scales: linear, 0.2, 0.4, 0.6, 0.8, 2nd, 3rd, and 4th power.

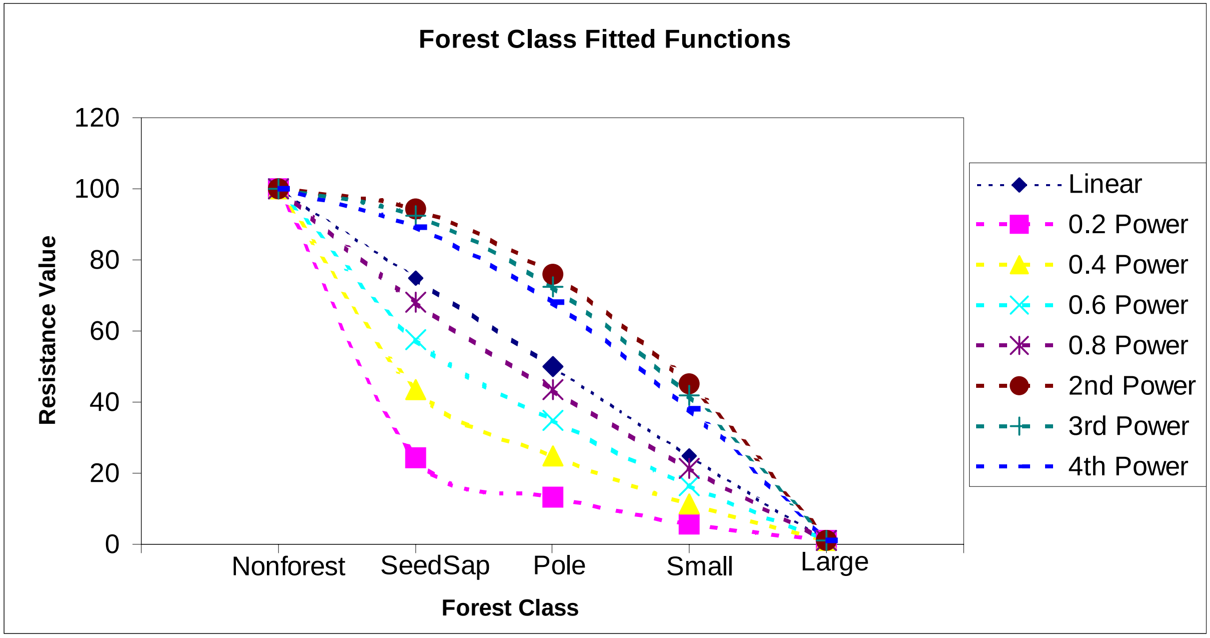

Figure 4: Power fitted functions for forest class based on 5 different classes, as related to resistance value on the landscape resistance map. Power functions are at 8 different scales: linear, 0.2, 0.4, 0.6, 0.8, 2nd, 3rd, and 4th power.

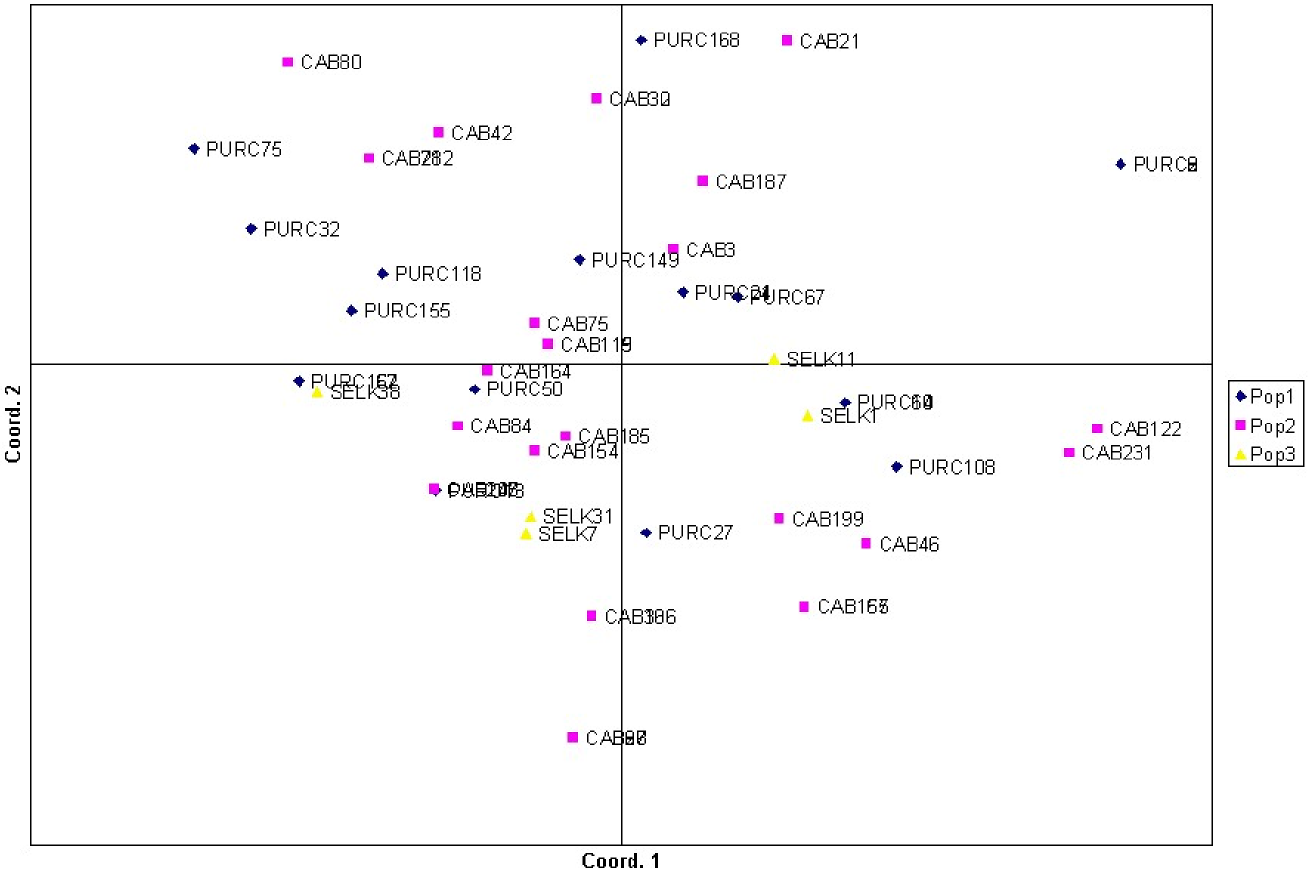

Figure 5: Results of PCA performed on all genetic samples collected in the IPNF and their corresponding location in the landscape based on UTM coordinates. Results indicate that there is little obvious genetic substructure of this population within the IPNF. This population may be best represented as a "genetic gradient" across the landscape rather than a discrete population.

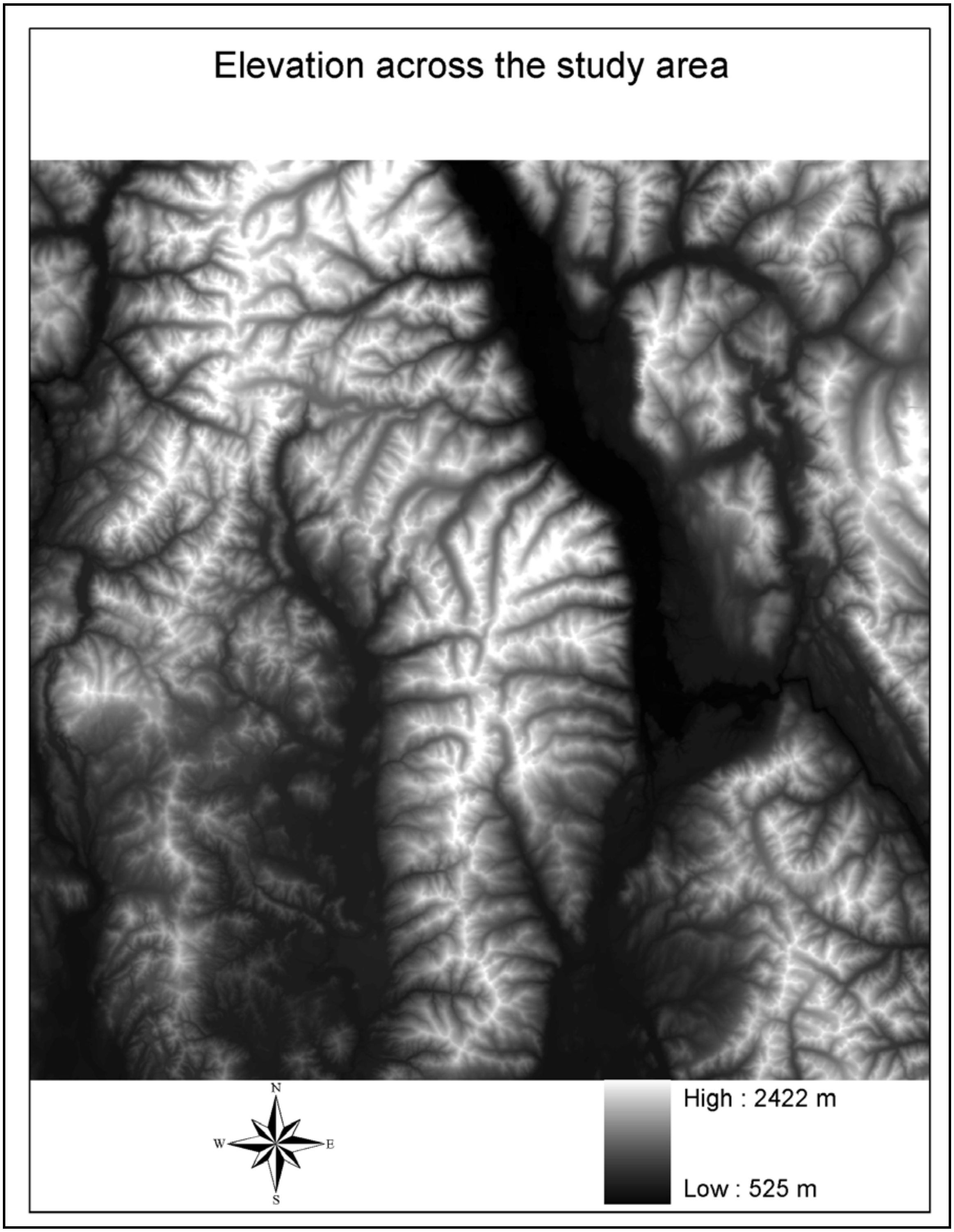

Figure 6: Digital Elevation Model (DEM) of elevation across the entire study area of the Idaho Panhandle National Forest in northern Idaho. Dark shaded area represent areas of low elevation while light areas represent high elevation.

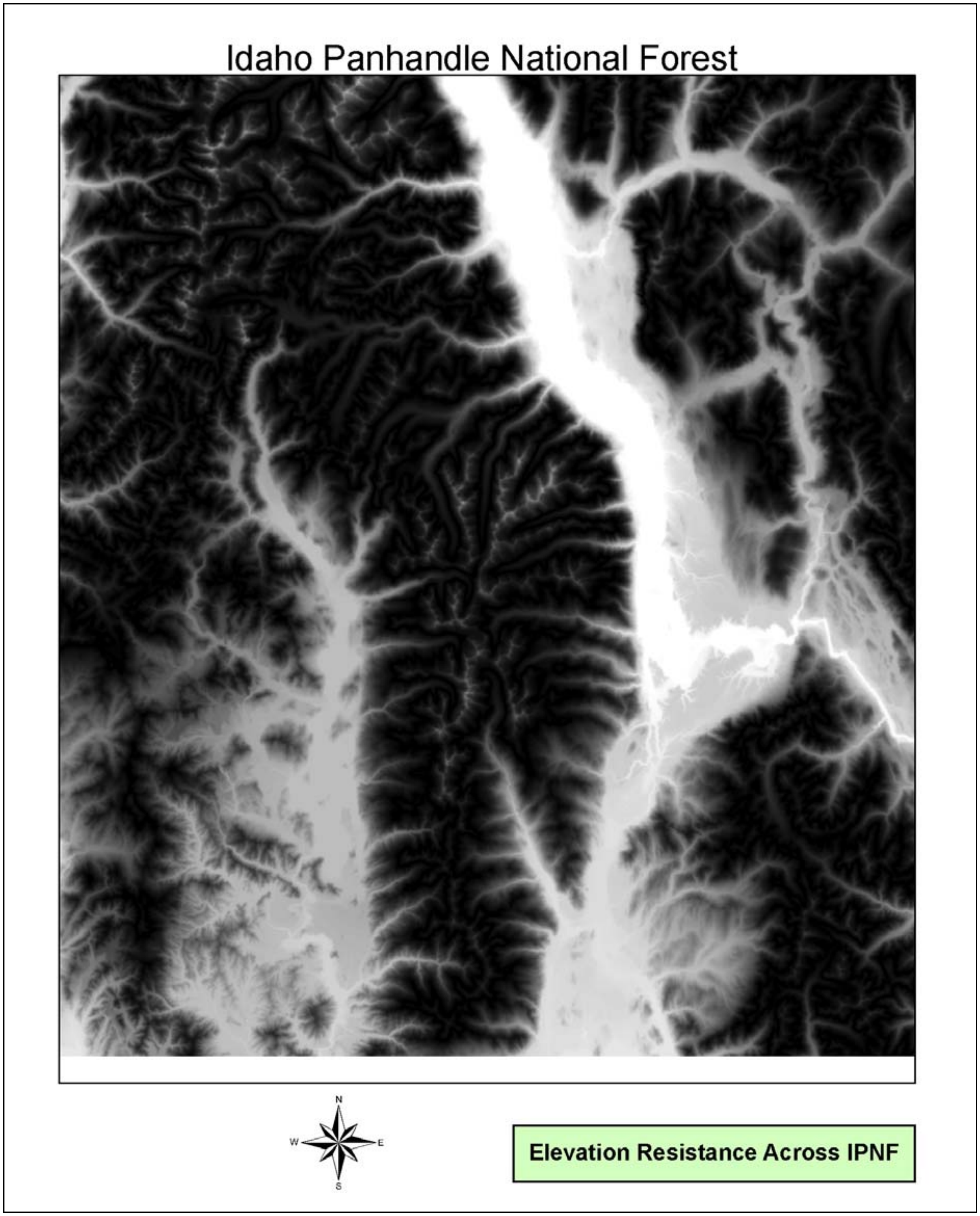

Figure 7: Visualization of the most supported model of landscape resistance, Elevation 1600m s.d. 600m (Table 13). This model depicts gene flow in the IPNF is strongly related to elevation, with movement facilitated at an optimum elevation of 1600m s.d. 600m. Dark areas represent low resistance to movement, while light areas represent high resistance to movement in relation to elevation across this landscape.

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