GRAPH-THEORETIC MODELING OF FUNCTIONAL HABITAT CONNECTIVITY FOR LYNX ON THE OKANOGAN HIGHLANDS, NORTHERN WASHINGTON

by

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Aaron Paul Jones
November 19th, 2004

To the rewilding of Turtle Island.

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ABSTRACT

Maintenance of habitat connectivity over various geographic scales is a conservation imperative for the long-term persistence of many species. Functional linkages for a given focal species may not be readily apparent or spatially coincident with explicit structural patterns in a landscape. In species-level habitat connectivity modeling, therefore, techniques derived from empirical data are needed to sustain a species-centric perspective on landscape mosaics.

This study demonstrates an empirically-based, combined Bayesian and graph-theoretic approach to modeling functional habitat connectivity. The case study focused on a subpopulation of Canadian lynx resident to a subalpine plateau in north-central Washington. Using data collected during two prior radiotelemetry studies, habitat selection by individual lynx was analyzed at two spatial scales using a combination of compositional analysis, χ^2 tests, and Neu's method. Significant habitat associations were used to create probability models for lynx presence using Bayes theorem. These provided a composite index of habitat suitability and enabled data-driven definition of habitat patches and an impedance surface for lynx movement in the study landscape. To address gradual variation in habitat quality, multiple study-wide and within-home-range patch surfaces were derived in accord with minimum percentages of areas of known lynx presence. Patches and cost-weighted interpatch distances were then converted to lattice data structures (graphs) and used as frameworks for hierarchical analyses of functional connectivity.

Mapped probabilities of lynx presence indicated higher quality habitat in the northward interior of the study area and in several drainages along its northern periphery. Areas most significant to study-wide connectivity were identified in terms of core linkages and those along which the habitat network is most susceptible to disruption. A general divergence between these areas suggests that the former, "parsimoniously-connected" cores of lynx habitat may also be the areas most resilient to fragmentation. Places where these areas co-occur, however, are "hotspots" supported by dual justifications for conservation prioritization. In measuring global connectivity, three indices were relatively insensitive to changes in patch surface definition until the graph based on seven percent areas of known presence was reached, after which point fragmentation was marked.

A critique of the Bayesian graph-theoretic modeling approach concludes the study, with emphasis given to its applicability for identifying subregional habitat linkages for far-ranging carnivores.

INTRODUCTION

Through adoption of a new modeling approach, this study seeks to assess functional habitat connectivity for a subpopulation of Canadian lynx *(Lynx canadensis)* on the Okanogan Highlands in northern Washington. To provide the requisite background on this problem, the following overview concerns: habitat connectivity, modeling techniques thereof, carnivores as focal species, selection of lynx as a target species, and the current scientific context in lynx ecology.

Habitat Connectivity and Fragmentation

Wildlife distribution and abundance have long been guiding concerns for conservation initiatives and related efforts in land management. In recent decades theoretical and practical developments in geography, landscape ecology, and conservation biology have spurred and supported more concerted investigations into the processes and structural characteristics of ecosystems that underlie and give rise to species distribution and abundance. These factors include, of course, animal movement in itself, and this has been a central focus of biogeographers for over a century. Only more recently, however, have naturally occurring patterns of species movement been seen in light of their direct conservation implications. Survival among individual organisms depends upon the ability to locate and utilize resources distributed across the landscape. More broadly, however, conservation genetics and metapopulation theory have established that, over various spatiotemporal scales, species movement potential is critical to the viability of individual populations, the persistence of metapopulations, and – ultimately – preservation of the evolutionary potential of species. To connote the degree to which a landscape facilitates (or hinders) natural scales of movement for groups of species and, more generally, the spatial continuity of natural cover types across a landscape, landscape ecologists have introduced the concept of *landscape connectivity* (Taylor et al. 1993; Noss and Cooperrider 1994; Soulé and Terborgh 1999). A more specific term, *habitat connectivity*, refers to the extent to which a landscape enables or impedes movements of individuals of a given species, either between vital resources (e.g., prey species, browse, water, or shelter) or between populations within a metapopulation (Noss 1991; Fahrig and Merriam 1985). Thus, habitat connectivity is both landscape-specific and species-specific, arising from the interaction between a landscape's composition and structure and the perceptual and movement characteristics of a species.

While habitat connectivity enables movement necessary to a population's self-regulating persistence, habitat fragmentation entails the limitation or preclusion of movement potential. Often correlated with loss in habitat area, habitat fragmentation refers to the functional isolation of habitat patches, by which interpatch movement is restricted and resource access and gene flow is reduced (Hanski and Gilpin 1997). For the species directly affected, other consequences of patch isolation may include: larger requisite home range sizes (with the result of greater energy costs for individuals); adverse edge effects (e.g., exposure to exotic or invasive species, security risks related to direct human impacts); behavioral changes (e.g., habitual avoidance of roads); altered patch composition due to changes in insolation, water, or wind flux; and reduced genetic diversity and its compensatory risks (e.g., disease susceptibility, inbreeding)(Noss 1992). If as a result of these cumulative factors the affected population is significantly reduced in size or extirpated altogether, the loss can trigger ecological imbalances which propagate through an entire ecosystem, potentially causing secondary extirpations or extinctions (Brown and Lomolino 1998) and, through positive feedback loops, continued ecological destabilization (Noss 1992). Because the functional isolation of habitat patches bears such consequences, efforts to assess, maintain and restore habitat connectivity are now recognized as critical to initiatives concerned with conserving species and ecological communities over the long-term.

Habitat connectivity is an emergent property of a species' experience of a landscape and, as a consequence, it is closely intertwined with questions of scale. Species perceive, move within, and choose their surroundings in a hierarchical manner (Johnson 1980; Orians and Wittenberger 1991; Aebischer et al. 1993; Bissonette et al. 1997; McClean et al. 1997). Individuals may respond to levels of landscape patchiness with different scales of movement (Kotliar and Wiens 1990; Pearson et al. 1996) and different needs may motivate selection of habitat types across various scales. For example, foraging decisions by lynx may occur at fine-scales, while location of a mate or establishment of a home range may occur over a far greater area. Additional scale-dependent limiting factors affecting species movement include temporal fluctuations in prey availability, density dependence (e.g., territoriality), behavioral avoidance of risk factors, and ongoing changes in landcover characteristics. Further, decisions and movements are likely to be affected simultaneously by factors occurring over fine and broad scales. Fine-scale movements during hunting, for example, are subject not only to the availability of foraging habitat across an individual's home range, but also to scale-sensitive processes and patterns at broader scales (e.g., disturbance regimes and associated fragmentation) that may directly or indirectly constrain the range of habitat types available at finer scales (Bissonette et al. 1997).[1] Conversely, broad-scale movements during mate location, dispersal, or migration are likely to be affected by fine-scale decisions in the assumption that foraging behavior occurs more or less continuously throughout these activities. Moreover, there may be a positive correlation between the spatial and temporal scales of an individual's actions, as is characteristic of many ecological processes (O'Neill et al. 1998). While foraging may occur throughout an individual's life and entail decisions with every stride, broad-scale movements associated with juvenile dispersal or mate location occur relatively infrequently in response to specific periods in an individual's life history.[2] Because its preconditions occur over the many spatiotemporal scales at which these species-landscape interactions take place, habitat connectivity is considerably more complex a phenomenon than might initially be apparent.

Multi-scalar Modeling of Habitat Suitability and Connectivity

To date there have been two primary paradigms for conceptualizing habitat networks and connectivity – that of *patch-corridor-matrix* models (Forman and Godron 1986) and that, more recently, of the *landscape mosaic* perspective (Wiens 1995). By either approach, examination of habitat connectivity asks the key heuristic question: "With respect to a species' use of habitat types, to what extent and by which configurations might it experience the landscape as spatially linked?" In seeking to answer this, both approaches also require definitions for habitat patch networks which, initially, are predicated in some fashion upon the definition and mapping of habitat quality.

A habitat suitability surface, therefore, is developed first as a simplified representation of a landscape mosaic that reflects how we may attempt to predict an animal's selection for habitat types across that landscape while engaged in foraging, denning, or other recurring activities. Because "habitat" and "non-habitat" are most often distinguished only over a gradient of habitat quality, this surface must depict the landscape in terms of relative habitat suitability or probability of species occurrence across space.

In a second phase, the patch networks are defined, consisting of patches themselves and the connections between them. The means of predicting networks differ between the two modeling paradigms, and are to be detailed subsequently (see Literature Review). Once these are articulated, however, network properties such as connectivity can be explored through the application of various metrics.

Ideally, both phases will involve representation of the landscape at multiple scales. Because species distribution is determined by hierarchically-based movement patterns, multi-scale analyses of habitat selection and habitat suitability are more biologically-realistic than single-scale analyses. Similarly, multi-scale analyses of habitat network connectivity are better suited to the many levels at which a species interacts with landscape composition and structure.

This study is developed in accord with this two-phased sequence and the landscape mosaic modeling paradigm. First, habitat selection is analyzed using a combination of telemetry locations of lynx and environmental data. Predictive surfaces of lynx habitat suitability are then developed through the application of Bayes theorem to significant habitat associations. The Bayesian outputs are used to model cost surfaces representing relative impedance to lynx movement in the interpatch matrix, while thresholds are applied to the same Bayesian outputs to objectively delineate the patches. In the second phase, patches and cost-weighted interpatch distances are converted into graph data structures that provide an analytical framework for assessing questions regarding habitat connectivity.

Scale-sensitivity is addressed in each phase. First, modeling of habitat suitability is premised on lynx habitat selection as analyzed at two biologically based spatial scales – selection for home ranges and that of areas within home ranges. Second, questions addressing functional habitat connectivity are considered at these scales as well.

Carnivores as Conservation Focal Species

Much of the scientific basis for conserving carnivores is reflected in their frequent treatment as focal species. By this designation, the specific needs of the individual species are used to frame the terms by which legal concerns, management objectives, and strategies to conserve biodiversity are construed. Focal species have been selected according to various criteria, including sensitivity to landscape change, as proposed by Lambeck (1997), and information content relevant to induction from the species' status to ecosystem-wide integrity. Based on these different rationales for designation, several terms have been used to describe focal species:

flagship species, indicator species, umbrella species, highly interactive species (formerly keystone species), ecological engineers, link species, and phylogenetically distinct species (Noss 1992). Of these, carnivores are often regarded as flagship species, indicator species, umbrella species, or highly interactive species.

Flagship species occupy a place in the popular cultural imagination that serves to inspire public support for conservation efforts. These are often "charismatic megafauna" and in North America include the grizzly bear (*Ursus arctos horribilis*) and cougar (*Puma concolor*).

Indicator species are those whose conservation status is thought to portend that of entire ecosystems. Due to their characteristically low population densities, low fecundity, and limited dispersal capabilities across exposed and developed landscapes, many carnivore species are particularly sensitive to broad-scale landscape change (Weaver et al. 1996) and, as a consequence, are often regarded as indicator species within the context of regional conservation planning. In particular, population viability among carnivores is often considered to reflect upon the degree of natural progression in landscape mosaics as well as other "higher-order" expressions of biodiversity.

Umbrella species are noted for having habitat requirements that encompass those of numerous other species. This is often the case with far-ranging species with large individual area requirements (i.e., so-called area-limited or dispersal-limited species); simply, the greater the scope of habitat required for residency, dispersal, or migration, the more likely a species' needs will spatially encompass those of other species. Because their high energy requirements necessitate relatively low densities and wide ranges, carnivores make archetypal umbrella species.

Highly interactive species, by definition, affect critical ecological processes or levels of biodiversity to a degree disproportionate to their own abundance in an ecosystem. Many top carnivores are considered as such in their communities because of the regulatory or structuring influence they exert upon populations of prey species. This is manifest in two ways. First, by regulating prey species abundances, dominant predators indirectly maintain the balance of trophic interactions that cascade downward through the food web. In the relative scarcity or absence of top carnivores – as in many historical cases of predator elimination – prey species fecundity and survivorship can explode in an effect known as herbivore- or mesopredator release (the "release" being that of limitation by predation)(Crooks and Soulé 1999). This can precipitate overexploitation of vegetation communities or rapid declines in songbird or small vertebrate populations (Terborgh et al. 1999). Second, in what is known as the *Paine effect*, carnivores can affect the diversity at a lower trophic level through "preferential feeding on a prey species that, in the absence of predation, is capable of competitively excluding other species that depend on a limiting resource" (Terborgh et al. 1999, p.45).

Canadian Lynx as a Target Species

Canadian lynx were chosen as the target species for two reasons – their suitability as a focal species for multi-species conservation goals and their threatened status in the contiguous U.S.

Arguably, lynx can be considered an appropriate umbrella species and under certain conditions *(*particularly at the southern periphery of their rang*e*), they may also function, per se, as a highly interactive species.

In Maine, Hepinstall and Harrison (2004) determined that lynx function as an umbrella species for six forest conifer-associated species, two forest hardwood-associated species, five forest generalists, and eight species associated with early successional forest. For regional conservation initiatives and studies of broad-scale habitat linkages for multiple species, recognition of lynx as an umbrella species may make strategic sense in two respects. First, as is typical of solitary felids, lynx are highly vagile and possess large spatial requirements (Ruggiero et al. 1994).[3] Both traits suggest that habitat utilized by lynx will coincide with those of more species than would, for example, that of another habitat specialist with more limited home range requirements and movement capabilities. Second, the topographic and vegetation characteristics of lynx habitat (generally – mixed-seral, boreal forestlands of higher elevations and low to moderate relief) is often incongruous with areas most preferred by other high-profile umbrella species such as the grizzly bear (*Ursus horribilis*) or elk (*Cervus elaphus*); consequently, lynx protection can serve to extend to ecological communities that might otherwise have been neglected by protective measures on behalf of the latter species.

While lynx may or may not trigger the Paine effect, they are "highly interactive" inasmuch as they indirectly influence the structure and composition of localized vegetation understories through their regulation of abundances of snowshoe hare, their primary prey. Where lynx still occur in the contiguous U.S., this influence may constitute a dominant ecological effect at finer scales (D.Gaillard, Program Associate, Predator Conservation Alliance, 10 May 2002, conversation).[4]

Beyond their suitability as a focal species for informing broader conservation efforts, the conservation status of lynx is itself a prominent concern in the southern extents of its range. Following the denial of two separate petitions (in 1992 and 1994) and several consequent lawsuits filed by conservation organizations, the U.S. Fish and Wildlife Service issued a proposed rule in June of 1998 to protect the lynx under the Endangered Species Act. An interagency lynx science team was appointed at the time to assess the scientific basis for conservation of these southern populations; their findings (as well as those of several associated researchers) were published in January of 2000 (see Ruggiero et al. 2000a) and were accompanied by a conservation strategy developed to provide consistent guidelines for management of lynx habitat. In March of that year, the species was officially Listed as Threatened under the ESA across its range in the contiguous U.S. (Notably, the ruling included a correlative mandate for the preservation of regional scale linkages for the species). In the years since, the elevated legal standing has drawn national attention to the status of the species, incited concerns over management implications of the Listing, encouraged an ongoing effort to reintroduce lynx in the Colorado Rockies, and highlighted the outstanding needs for more empirical knowledge on the species and particularly on the ecology of southern populations. In January of 2004, the Northern Region of the U.S. Forest Service released its Draft Environmental Impact Statement (DEIS) for the Northern Rockies Lynx Amendment, by which the USFS and Bureau of Land Management have proposed to amend extant land management plans for eighteen National Forests and four BLM units in accord with guidelines for management of lynx habitat. A similar DEIS soon followed for amending plans on federal lands in the Southern Rockies.

Scientific Context

Efforts to provide for the conservation of southern populations of lynx are confounded by formidable knowledge gaps regarding lynx ecology (Ruggiero and McKelvey 2000). As of April 2002, the entirety of published research on lynx in the U.S. have been based on only seven studies (Koehler et al. 1979; Koehler 1990; McKelvey et al. 2000b; McKelvey et al. 2000c; Mills et al. 2000; Squires and Laurion 2000; Schwartz et al. 2002), with relatively few studies having been published on the ecology of southern snowshoe hare populations. Considerable research does exist on both species in Canada and Alaska. Significant demographic differences are known to occur, however, between northern and southern lynx populations, while marked differences exist in landcover configuration between lynx habitat in the taiga and in remnant pockets of high-elevation habitat in the south. Therefore, the applicability of studies of northern lynx populations to conservation of southern populations remains unknown.

Even while researchers have a general understanding of lynx habitat associations in the southern extents of their range, there are often considerable discrepancies between what is conventionally regarded as suitable and accessible habitat and the actual presence of lynx. These inconsistencies are also manifest in the modeling criteria used for predicting habitat for lynx in the lower latitudes. Although the ESA Listing required determination of a federal protocol for mapping lynx habitat, its guidelines appear to lack sufficient rigor and consistency – a contention supported in evidence by the clear alignment of distinctions in predicted "habitat" and "non-habitat" with boundaries separating adjacent National Forests.

Such incongruities serve to underscore our lack of knowledge regarding lynx metapopulation dynamics and other factors influencing lynx distribution and abundance (Ruggiero and McKelvey 2000). By extension, virtually nothing is known regarding the implications of specific habitat configurations for lynx, and landscape-level studies have yet to establish specifics of how lynx ecology and population persistence are affected by habitat fragmentation (Koehler and Aubry 1994). Nevertheless, we can state that, as far-ranging habitat specialists (O'Donoghue et al. 1998) and as a rare species often associated with wilderness conditions, it is likely that lynx are susceptible to anthropogenic fragmentation of habitat (Andrén 1994). Landscape-level habitat fragmentation is indeed believed to adversely impact most far-ranging carnivores (Beier 1993; Noss et al. 1996; Soulé and Terborgh 1999; Crooks 2002), and as the apparent decline in southern lynx populations remains unexplained, it is only sensible to proceed by the precautionary assumption that the maintenance of landscape-level habitat connectivity is important for lynx persistence.

Although a critical component of this task, predictive modeling of lynx habitat connectivity must be tempered to the current limitations in field research on the species. More specifically, the complexity of the models must match their intended use and be supported by the nature of the data. Because actual habitat connectivity is inextricably related to a species' movement patterns, one might expect that, in general, dynamic simulation modeling would be best suited to exploring the topic. However, location data on wide-ranging species remains exceptionally labor-intensive and expensive to secure (Beier 1996) and is often unavailable at the temporal resolution or duration required to support a dynamic movement component to connectivity analyses. This has most often been the case with field data on felids and other carnivore species, whose rarity, naturally low densities and elusive behavior further complicate attempts to track their movements. Consequently, in such cases – this study included – connectivity must be assessed for the time being through the atemporal spatial patterns and associations found in location data.

Although restricted to static models, an effort was made in this study to provide a hierarchical assessment of connectivity in the spatial dimension through scale-specific analyses of habitat selection and iterative manipulation of dispersal-distance functions. The graph-theoretic modeling approach used for the study can provide an effective means of spatial pattern recognition as well as a heuristic framework for future analyses of functional connectivity (Urban and Keitt 2001). Thus, even while temporally static, the models can provide useful insights into the more enduring spatial characteristics of the landscape that continue to give rise to functional habitat connectivity for lynx.

Objectives

The cumulative goals of this study were twofold: first, to provide for improved understanding of functional habitat connectivity for resident lynx on the Okanogan Highlands; and second, to demonstrate the application of a combined Bayesian and graph-theoretic habitat modeling approach. Toward these ends, the study's methodology is framed by six more specific objectives. Of these, the first implicitly addresses the uncertain defensibility of the federal mapping protocol for defining suitable lynx habitat. The remaining objectives regard lynx habitat connectivity.

1) Development of an objective, data-driven prediction of lynx habitat suitability across the study area.
2) Measurement of the extent to which the study area is functionally connected for lynx.
3) Evaluation of the sensitivity of selected measures of connectivity to various patch definitions.
4) Identification of areas that compose core linkages of connectivity across the study area and within individual home ranges.
5) Identification of areas that constitute weakest links in connectivity across the study area and within individual home ranges.
6) Mapping of areas that appear most critical to preservation of study-wide, multi-scalar habitat connectivity for lynx.

Thesis Structure

Chapter 2 begins with a review of literature characterizing landscape ecology as the investigative context for this study. This synopsis highlights the field's geographical roots and illustrates the role that scale plays as a central organizing concept to landscape ecological inquiry. This is followed by a review of the patch-corridor-matrix and landscape mosaic conceptualizations of landscape connectivity and the modeling techniques characteristic of each perspective. The remainder of the literature review presents supportive material specific to the modeling approach adopted in this study. This includes information on the nature of and precedents in Bayesian habitat suitability modeling, as well as an introduction to graphs and graph-theoretic modeling of landscape and habitat connectivity.

With this as theoretical background, Chapter 3 introduces the case study with a description of the study area and field data, a review of the available literature on lynx ecology with respect to the identification of predictor variables, and a description of the selected datasets for these variables. Chapter 4 details the methodology adopted, including habitat selection analyses and the Bayesian and graph-theoretic modeling phases of the study.[5] Results are presented in Chapter 5. Chapter 6 begins with their interpretation and a discussion of the implications for lynx conservation in the study area. Data needs are then enumerated, along with a discussion of further modeling prospects which additional data might support. The Bayesian graph-theoretic modeling approach is then evaluated and followed, in conclusion, by recommendations for its use in other instances in Chapter 7. Finally, notes, cited references, and appendices are provided.

LITERATURE REVIEW

Landscape Ecology

Since recognition of landscape ecology broadened significantly in the 1970s (Wiens 1999), the defining nature and content of the field has been subject to a considerable diversity of opinion (Turner et al. 2001). While this may be distinctive to all young sciences in their exploratory stages, the strength of ongoing theoretical development in the field is amplified by its multi-disciplinary groundwork and the close tie between its theory and practice. Despite its swift evolution and fluid boundaries, one can nonetheless distill a working characterization of the field.

At its core, landscape ecological research concerns the reciprocal interactions between the spatial composition and configuration of landscape mosaics and ecological processes. Implicitly, this involves consideration of the causes and consequences of landscape heterogeneity across a range of spatial and temporal scales. Also of note is a proclivity among its practitioners to be as concerned with application of emerging analytical techniques and software as with development of the field's core theory.

The growth of the science has been spurred by widening recognition of the importance of spatial and temporal scale-dependencies in ecosystems and their implications for the success of conservation strategies, land management scenarios, and land use plans. In coming to adopt a decidedly systems approach to landscapes, conservationists, managers, and planners increasingly require that landscape ecological research provide specific principles and pragmatic guidelines to inform their work. To support this end, dialog with researchers is essential (Wu and Hobbs 2002).

A Field Between Disciplines

Research questions in landscape ecology rely on the application of a diverse set of tools and often benefit from various modes of inquiry. Both theoretically and methodologically, landscape ecology rests at the convergence of geography, (macro-) ecology, conservation biology, spatial statistics, and advances in information technology (e.g., GISystems; remote sensing).

The very multifaceted nature of the field exemplifies its earliest historical emergence in the modern European tradition of geography.[6] From what might now be referred to as a holistic, resource-management perspective, early 20th century geographers in Central and Eastern Europe approached landscapes through the integrated study of ecological processes and anthropogenic impacts on the land (Wiens 2002). Out of this context, German biogeographer Carl Troll declared in his 1939 work Landschaft Ökologie (Troll 1939) the genesis of a new field of study. "Landscape ecology", Troll maintained, represented a distinct convergence of all methods of natural science, from the science of forest vegetation and aerial photo interpretation to geography as a "landscape science" and "ecology". As such, landscape ecological research produced literature (in both German and Dutch) within Europe until the early 1980s, at which point English translations emerged and the discipline was taken up in North America as well. At present – and especially among Europeans – landscape ecology continues to represent the tradition of integrating geography and ecology in a holistic approach to landscapes and ecosystems (Wiens 1999).

Another precursor to theory and practice in contemporary landscape ecology has been biogeography, the science that seeks to document and understand spatial patterns of biodiversity (Brown and Lomolino 1998). Biogeography thus shares with landscape ecology an explicit concern for the effects of spatial heterogeneity and landcover change in shaping species' distribution and abundance. Perhaps its most important influence over landscape ecology has come in the Theory of Island Biogeography. Also significant, however, has been a characteristic attention within biogeography to the ramifications of scale. Scales of analysis within academic and applied biogeography alike range – just as do measures of biodiversity – from the genetic level to the biospheric. Temporal scales of analysis are just as variable, running from nearly atemporal or static analyses of distributions at the moment of their sampling or estimation to consideration of the evolution of phenomena across geological timeframes. This variability has attuned many biogeographers to the implications ecological complexity holds for scale-sensitive analyses and has highlighted the imperative of framing landscape-level research from a multi-scalar standpoint. While specific scales of analysis often differ in landscape ecology in accord with the disciplinary background of individual investigators, the importance of multi-scalar approaches to landscape pattern and process have generally been embraced as a central tenet within the field.

Many landscape ecologists might characterize their field as much by the tools used as by the conceptual framework shaping its research (Wiens 1999). Among these tools, geographic information systems (GISystems) have been instrumental in facilitating the exploration and analysis of spatial data over large extents of the Earth's surface systems. The ability to take advantage of the ever-increasing abundance of remotely sensed imagery, in particular, has afforded an invaluable and efficient means of investigating landscape patterns and processes across the wide array of spatiotemporal scales relevant to landscape mosaics. GISystems emerged in the 1980s as a convergence of parallel developments in automated spatial data capture, analysis, and presentation within several fields, including: geography and cartography, land use planning, spatial statistics, remote sensing and image analysis, surveying and photogrammetry, geology, hydrology, the soil sciences, and civil engineering (Burrough and McDonnell 1998). With the exponential growth in use of GISystems over the last two decades, problems surrounding the properties and handling of geographic information have become increasingly important. Issues related to the accuracy, cognition, representation, standards for exchange, and societal applications of geographic information, as examples, have been brought to the fore. In the mid-1990s, the term geographic information science (GIScience) arose to denote the study of these and other problems inherent to the use of GISystems. In 1996, the University Consortium for Geographic Information Science (UCGIS) articulated a series of core research priorities for the field with the aim of improving our overall understanding of the nature of geographic information and the means for its effective use. As a discipline in which the use of GISystems is ubiquitous, landscape ecology stands to benefit greatly from this work.

Beyond its geographical underpinnings and intrinsic reliance on geographic information, landscape ecology is also characterized, in practice, as a mode of traditional ecology extended to broad spatial contexts. In this light, the field is highly akin to macro-ecology, while exhibiting further theoretical parallels with population- and community ecology. The embrace of landscape ecology by an increasing number of ecologists has required a re-evaluation of many principles of traditional ecology that promises to catalyze a paradigm shift across many other ecological subfields (Ingegnoli 2002). Beyond a focus on broad scales of observation and analysis, this transformation has entailed an explicit recognition of the importance of pervasive interactions between spatial pattern and ecological processes (Pickett and Cadenasso 1995). Spatial configuration is already considered integral to theories regarding processes that occur across many levels of ecological organization, from genes to individuals, to populations and communities (Wiens et al. 1993). In addition to reassessment of the effects of scales of analysis and of spatial heterogeneity, landscape ecology implicitly requires that ecologists recognize the new scientific paradigms of chaos and complexity theories and modify many classical ecological definitions and principles that are too limited to apply to complex systems (Ingegnoli 2002).

In addition to guiding purely academic research, landscape ecology is of imminent relevance to applications in conservation and land management. Questions raised in the field continue to instill awareness among conservationists and managers to the importance of historical disturbance regimes, species dispersal dynamics, and spatial heterogeneity in landcover to ecological integrity. Perhaps most importantly, the field has advanced the wide adoption of a "landscape scale" perspective on matters of biological conservation. The framing of ecological questions in more extensive spatial and temporal terms has formative consequences for the planning and implementation of conservation and management strategies. Conservation goals, for example, have broadened to encompass provisions for maintaining long-term metapopulation dynamics and for sustaining evolutionary potential (Grumbine 1994). Further, under the rubric of "adaptive ecosystem management", one now witnesses the institutionalization of a fundamental shift in perception from the notion of the "balance of nature" to one of the "flux of nature" (Pickett et al. 1992; Pickett and Ostfeld 1995).

With these emphases on "thinking like a mountain" (Leopold 1949), landscape ecologists have a kinship with conservation biologists. A mission-oriented discipline, conservation biology comprises both pure and applied science in dedication to the preservation of biological integrity and diversity. As a pure science, it draws considerably from: island biogeography and biodiversity mapping; evolutionary-, population-, community-, and physiological ecology; phylogenetics, evolutionary- , behavioral- , molecular- , and wildlife-biology; and statistics. In its practical capacity, conservation biology's similarities with landscape ecology are readily apparent. Research emphases in both disciplines have frequently been adapted to applications in conservation area design, ecological restoration, and natural resource planning and management. Further yet, problem definition and methodologies in both disciplines are often characterized by a holistic integration of ecological and socioeconomic factors.

Given its firm grounding in ecosystem science, conservation biology's contributions to landscape ecology have been distinct. Population viability analyses, wildlife genetics, and metapopulation dynamics, in particular, have been integrated into descriptive, predictive, and decision-theoretical models of landscape pattern and composition (Gustafson 1998). The concepts and lexicon of metapopulation theory, in particular, have been widely adopted within landscape ecology (Turner et al. 2001). Conversely, landscape ecology has been recognized for two specific contributions to conservation biology. First, it has provided the working concept of the *landscape mosaic*, referring to a patch-corridor-matrix model for landscapes that is applicable across multiple scales, from the microscopic to the continental (Forman 1995). Second, it has popularized use of the "landscape-scale" of analysis (Forman 1995).[7] This Forman described as the spatial scale at which human impacts on evolutionary processes tend to be particularly salient (e.g., anthropogenic habitat fragmentation; homogenization of ecosystems; alteration of natural flows and disturbance regimes) and at which many biological conservation initiatives are, by consequence, articulated.

Insofar as it has been independently taken up by researchers working within the separate and more-or-less formalized pursuits of geography, ecology, or conservation biology, landscape ecology currently remains a primarily multi-disciplinary venture (Wu and Hobbs 2002). For it to fully mature as a more integrated and interdisciplinary science in its own right, Wu and Hobbs (2002) contend, cross-disciplinary fertilization and collaborations must be actively encouraged. If there is a singular quality to landscape ecological research that can best serve as an organizing principle in such a synthesis of the discipline, it may be the propensity to identify and define problems from the outset with an emphasis on the complex, scale-sensitive, spatiotemporal patterns of landscape mosaics (Risser et al. 1984; Turner et al. 2001).

A Central Concern for Scale

While an *a priori* focus on patterns in landscape mosaics may be the trait that most clearly distinguishes landscape ecology from other disciplines, concern for the effects of scale on biological interactions is increasingly a core stimulus in shaping landscape ecological inquiry. This is indeed the case across a wide range of research foci in the discipline, including those on: landscape structure, landscape dynamics, land-use and landcover classification, biodiversity, habitat analysis, animal and plant ecology, climate modeling, biogeochemical cycles and energy flows, land-use planning and land management, and scale itself (Withers and Meentemeyer 1999). Technological and conceptual tools used to analyze scale effects are similarly diverse, and include: geographic information systems, remote sensing, spatial statistical models, simulation models, fractal geometry, Spatially Explicit Population Models (SEPMs), hierarchy theory, and hierarchical research design.

Although the importance of scale effects is now well recognized, the challenges to their study remain formidable. Early in the spatial analysis tradition of geography, Haggett (1963) identified three of the most significant “scale problems”: the scale coverage problem (i.e., that of spatial extent), the scale linkage problem (i.e., that of scale-specific observation and resulting scale-sensitive datasets), and the scale standardization problem (i.e., that of extrapolating analyses across spatial scales and across different regions). Each of these problems is complicated by the presence of spatial heterogeneity and nonlinear dynamics within landscape systems.

One response to these challenges has been to emphasize an intermediate spatial scale of observation and analysis that correlates strongly with many aspects of human perception and agency. This is the aforementioned landscape-scale asserted by Forman (1995) to be the optimum scale for framing land management and conservation planning. Research design at the landscape-scale may improve its direct utility for these applications, while the standardization of that practice can also expedite cross-study comparisons.

Yet, however practical it may be to include as a sort of benchmark scale of reference, any well-considered research in landscape ecology will not rely solely upon this or any other single scale of observation. An appreciation for the scale-sensitivity of sampling schemes and analyses is critical in the field because patterns in complex natural systems emerge from processes that occur across many spatial and temporal scales (Levin 1992). Indeed, as one of the principal ways by which ecological complexity finds expression, scaling phenomena pose definitive challenges for both the theory and practice of landscape ecology. On one hand, scale-dependencies complicate theoretical development in that they often confound traditional hypothetico-deductive approaches (Wiens 1999); disproving a null hypothesis, that is to say, becomes a difficult affair when process-pattern relationships are likely to be highly sensitive to the spatiotemporal scale(s) of one's observations. The complexities of cross-scale dependencies also magnify the difficulty of experimentation and replication at landscape-level or regional scales; effective controls for experiments become untenable, and samples that are not truly independent invite the pitfall of "pseudoreplication" (Hargrove and Pickering 1992). If complexity is the nemesis of theory, it is also as much for practice, and researchers remain uncertain of the extent to which they can safely simplify their means of interpreting scale-sensitive spatial patterns and processes (Wiens 2002).

The problems of scale-sensitivity and cross-scale dependence are closely related and each underlies many practical concerns within landscape ecology. In the effort to contend with these matters (and, by extension, that of cross-scale extrapolation) more effectively, some landscape ecologists have sought insights from hierarchy theory, a conceptual framework articulated by Allen and Starr (1982) and O'Neill et al. (1986) to characterize systemic relationships occurring between various hierarchical levels of biological organization. Addressing the classic middle-number conundrum of ecology (Allen and Starr 1982; Wiens 2002), hierarchy theory posits that the dynamics of a system at an intermediate (or, focal) level can be explained by the behavior of components acting at finer and broader scales. Processes at lower levels are considered to act as mechanisms that give rise to intermediate-level phenomena, while patterns at higher levels are understood to act as constraints on the potential range of their expression. Following on general systems theory (von Bertalanffy 1973), hierarchical levels are distinguished by the different spatial scales and frequencies at which their characteristic processes tend to operate. Further, these spatial and temporal scales are often themselves linked, in general, through positive correlation (Delcourt and Delcourt 1988); thus, lower-level processes typically occur at high frequencies and fine extents, whereas upper-level processes tend to occur at slower rates and across broader extents. Another key principle inherited from general systems theory states that as one progresses to increasingly broader scales, natural systems yield emergent properties that cannot be fully explained through interpretation of mechanisms operating at finer scales. Last of note, hierarchy theory adopts from Koestler (1969) the concept of the *holon*, referring to an entity or component that, at any given hierarchical level, functions at once both as a composition of parts and as a system in its own right. Given that biological levels and spatiotemporal scales are strongly correlated, these and related ideas regarding systems behavior have been provocative for many landscape ecologists in their continuing investigations of scale. In practical terms, hierarchy theory has provided the field with several important guidelines, including the need that research be conducted directly at the scales at which phenomena of interest occur, as well as the need that one re-assess relevant ecological processes with changes in spatial scales of interest. In a general sense, hierarchy theory has also provided a rough, conceptual touchstone by which landscape ecologists have derived qualified insights regarding the nature of scale-sensitive phenomena and cross-scale dynamics within landscape mosaics. The theory has not, however provided a methodological framework for ecological scaling (Wiens 1999).

Given that most ecological measurements are made at relatively fine scales, the exploration of techniques of extrapolation remains a key research priority for landscape ecologists. Simple multiplicative or additive approaches have formed the groundwork for many of the various methods to date (Wiens et al. 1993). All such strategies must cope with the challenges of estimating and scaling up spatial heterogeneity, a prospect that is only confounded by the presence, in most landscapes, of nonlinear relationships across scales. Out of the search for rule-based techniques in the face of these complexities, researchers have explored the idea that in a given landscape mosaic, certain ranges, or *domains,* of scales exist within which extrapolation may be practical despite the presence of nonlinearities throughout the system writ large. Domains of scales, as such, are therefore distinguished by thresholds in scale dependencies at which nonlinear shifts in patterns or processes occur (O'Neill 1979; Wiens 1989). Identification of these thresholds is problematic. However, some progress has been made on this front through the application of fractal theory. Originally formulated by Mandelbrot (1967), the theory states that power-law statistics can be used to quantify changes in the properties of open, complex systems that occur across scales at many orders of magnitude. Because such systems (landscapes included) exhibit self-organized criticality (Bak and Chen 1991), they are self-similar across certain scales (Grumbacher et al. 1993). Each range of self-similarity represents a domain of scale within which landscape pattern or process is considered scale independent and extrapolation is possible using a scale-invariant measure such as the fractal dimension D or a lacunarity index (Plotnik et al. 1993). Fractal theory maintains that the power-law relationships provide a direct means of identifying domains and their limits – whereas a power-law will hold over self-similar scales, its disruption marks the thresholds that distinguish them. Fractal-based extrapolation has proven to be a useful strategy under certain conditions. However, in cases involving major changes in upper-level constraints, its efficacy is likely to be significantly compromised (Turner et al. 2001).

Although concerted attention to the ramifications of extrapolation serves to underscore the central tenet in landscape ecology that “scale matters”, these efforts – as with hierarchy theory – have, to date, only hinted at an articulated theory of scaling (Wiens 1999). In lieu of such a theory, the immediate need to address ecological complexities more effectively has prompted a movement within landscape ecology toward the use of research designs that explicitly integrate multiple scales of observation and analysis (Bissonette 1997).

Although this brief review has emphasized the formative role of scale issues in shaping landscape ecological inquiry, the field is characterized by numerous other themes, including: a focus on the effects of spatial configuration and variation, an overt recognition of the analytical implications of spatial and scalar complexity in ecosystems, a relative openness to cross-disciplinary collaboration and borrowed methodologies, and an opportunistic implementation of rapid technological advances in spatial data collection and analytical capacities.

Interpreting Connectivity

Interpretation of habitat connectivity within a modeling environment requires that it be regarded as one metric (among many) for describing landscape structure. In contrast with a majority of spatial statistics that quantify landscape structure based on sampled data, landscape metrics describe the spatial properties of mapped data, as in the case of a patch network within a landscape mosaic.

Island-biogeographic Theory

One way of formulating a landscape connectivity metric has been to focus principally on the structural properties of mapped data. A prominent framework for characterizing habitat connectivity – known widely as the patch-corridor-matrix model (Forman 1995) – relies on such a structural approach and has its origins in island-biogeographic theory. In their seminal publication The Theory of Island Biogeography, MacArthur and Wilson (1967), spurred by models of dynamic equilibria in other fields, instigated a pivotal shift in biogeography away from idiosyncratic and static approaches to a means of associating broad patterns in species distributions with general ecological explanations. The shift represented a new bridge between traditional biogeography and ecology.

Central to the Theory of Island Biogeography is the characterization of three key mechanisms affecting species abundance and distribution on islands. First is the species-area relationship, whereby species number tends to increase with increasing area. Second is the species-isolation relationship, whereby isolation increases the slope, or rate of increase, of the species-area relationship. And third is the rate of species turnover, by which, in a stable-state island ecosystem, continual replacement of species through cyclic colonization and extinction events contributes to equilibrium of species richness in a stable-state island ecosystem (MacArthur and Wilson 1967).

These mechanisms formed the groundwork for articulation of what has since been denoted as Wilson's *taxon cycle*. By this, MacArthur and Wilson postulated that an island reaches dynamic equilibrium in population size and species diversity through iterative processes of migration and extinction. The arrival of new species from a source area (i.e., a mainland), that is, was thought to be balanced by the extinction of other island species due to competition, genetic inbreeding, or natural disaster.

MacArthur and Wilson acknowledged several assumptions necessary to definition of the taxon cycle: (1) insular speciation would not occur; (2) immigration and extinction rates were independent of area and non-species-specific; (3) insular biotas were in equilibrium over evolutionary time; (4) extinction is affected only by area; and (5) immigration is affected only by relative isolation. Additional confounding factors have also been cited, including the effects of interspecific competition, variable habitat quality, disturbance regimes, and trophic dynamics, among others.

Even with these assumptions, the taxon cycle had proven instrumental in biogeography and there followed near universal agreement on the provocative importance of their work. In its elegant simplicity, the Theory of Island Biogeography stimulated thousands of research efforts that sought its application, validation, refinement or modification. Interest in the species-area and species-isolation curves, in particular, eventuated in four fundamental criteria for determining the rate of the taxon cycle: island area, island isolation (from a mainland), connectivity (with a mainland), and circuitry (between islands).

Island Area. Generally stated, as area decreases, so does habitat diversity, and, in turn, species diversity. Smaller areas support fewer individuals of any given species, while smaller populations are more extinction-prone due to being more susceptible to sex or age fluctuations, genetic inbreeding, environmental changes, and natural disasters (Soulé 1986). Consequently, biogeographers argue that smaller islands are less able to support high levels of population density and species diversity.

Island Isolation. The frequency of successful immigration is dependent upon the relative isolation of an island from its mainland species source. A large island close to the source, that therefore, will support more biodiversity than a remote island of identical size simply by reason more species being able to reach it.

Connectivity. Clearly, the degree to which an island is connected to the mainland affects the degree of isolation. The two most common forms of this connectivity for islands are land bridges and series of other islands acting as intermediaries (or, “stepping stones”).

Circuitry. Also influencing the effects of island size and isolation is the circuitry, or alternate routes or loops, present between islands or between an island and its mainland. These alternate routes increase the chance of successful immigration, both by providing a higher probability of that an individual animal will encounter a corridor and also by spreading the stochastic risks involved with dispersal across different paths. The presence of circuitry implies that of “connectivity” (as defined above), but connectivity doesn’t in itself indicate circuitry.

The Patch-corridor-matrix Model and Structural Connectivity

Biogeographers and conservation biologists soon recognized the lessons that island-biogeographic theory might hold for understanding species abundance and diversity in terrestrial ecosystems. In their relative isolation to one another, habitat patches, parks, and reserves were perceived as analogous to actual oceanic or continental island ecosystems, whereby “islands” of habitat were situated in “seas” of inhospitable “non-habitat”. Following on MacArthur and Wilson’s principles regarding island area and isolation, conservationists argued that as habitat “islands” diminished in size and increasingly insularized through fragmentation, they would experience concomitant declines in species diversity. With habitat fragmentation recognized as a prime factor driving accelerating extirpations and extinctions of native species, many saw protection and restoration of connectivity and circuitry as essential to the preservation of various levels of biodiversity and the long-term population viability of many species. It was also understood that sustaining connectivity would help mitigate for losses in total habitat area.

Presaging what Forman (1995) would describe as the patch-corridor-matrix model, a new lexicon emerged by which habitat islands were described as patches or (at broader scales) *core-areas,* effective connections between them denoted as *corridors*, and the intervening "non-habitat" labeled the *matrix* (Noss 1992). Drawing initially from island-biogeographic theory and the patch-corridor-matrix conceptual model, conservationists began to formulate principles to guide the identification of interconnected networks of habitat (see Diamond 1975)[8] in what has since become known either as conservation area design or wildland reserve design (Noss 1992). From this early thought on network design until the arrival of metapopulation models in the late 1980s, much of the discourse in conservation biology was suffused in island biogeographic theory and an emphasis on species-area and species-isolation relationships (Hanski and Gilpin 1997). The arrival of metapopulation theory signaled a shift in the discipline whereby habitat networks came to be conceived in terms of species subpopulations or metapopulations that persist in separate habitat patches and yet which are interlinked by occasional interpatch movements (Hanski and Gilpin 1997; Hanski 1998).

This transition was expedited by the ability of specific metapopulation models to yield system- and site-specific recommendations that surpassed generalized principles of reserve design (Hanski and Gilpin 1997). Although metapopulation theory may have largely eclipsed island biogeographic theory as the framework within which most questions of reserve design are considered, it, as well, is predicated on the patch-corridor-matrix characterization of the landscape mosaic (Hanski 1999).

Whether framed by island biogeographic or metapopulation theory, reserve design has been based on the contention that corridors function to facilitate movements of organisms between habitat core areas or patches. These include dispersal events, defined as stochastic, intergenerational movements between major habitat patches or subpopulations. Dispersal sustains gene flow to relatively small, isolated subpopulations that may be experiencing inbreeding depression and it is the naturally-occurring mechanism for the recolonization of patches after local extirpations (Noss 1987; Beier and Noss 1998). Intrinsic to metapopulation dynamics and a key to survival for many species inhabiting fragmented landscapes (Opdam 1990), dispersal is critical to ensuring genetic variability and the long-term viability of self-regulating populations of wide-ranging species (Hansson 1991; Noss 1992; Noss and Cooperrider 1994; Noss et al. 1997; Soulé and Terborgh 1999a, b). In addition to dispersal, Noss (1992) has argued that corridors allow for seasonal movements of species as well as potential long-distance range shifts that may be necessitated by climate change.

Beyond corridors, the connectivity of wildland networks is thought to benefit, to a lesser extent, from the presence of stepping stones – habitat patches that, although discontinuous, can nonetheless provide for effective movement between core areas. In addition to connectivity, conservation planners have also recognized the importance of maintaining circuitry to counter habitat insularity. If core-areas are relatively clustered and interlinked with multiple loops and alternative pathways, movement potential is thought to extend in multiple directions, increasing the frequency of interpatch interactions and, therefore, that of gene flow (Noss et al. 1997).

Today, as science-based conservation has propelled a valuative and cognitive shift in society from emphases on scenery and sites to biodiversity and systemic networks, reserve design has similarly matured to address the complexities at the interface of socioeconomics and ecological realities. Beginning with the essential patch-corridor-matrix conceptualization of landscapes, reserve design has evolved to address the entire landscape mosaic, specifying properties and configuration of reserves as well as suggesting compatible uses for proximate lands in the matrix.

(Wiens 1999). For well over a decade, organizations such as the Wildlands Project (2002) and the Yellowstone-to-Yukon Conservation Initiative (1997) have worked to develop spatially explicit strategies for maintaining and restoring regional habitat networks as based, principally, on the patch-corridor-matrix model (see Noss 1992). More generally, the corridor concept is actively being applied at an international scope with the design and implementation of greenways (North America, Australia, and European urban regions), geoecological networks (Eastern Europe), and bioecological networks (Western Europe, Africa, and Australia).

As these efforts progress, many continue to debate the efficacy of corridors and the costs and advantages in using them as a framework for conservation planning. Many of those who advocate for corridors do so out of the conviction that they are necessary to sustain (or restore) natural scales in the abundance and distribution of native wildlife species across landscapes. Cited disadvantages to corridors include the possibility of their acting as mortality sinks or as conduits for the spread of disease, pests, or exotic species (Hobbs 1992; Hobbs and Wilson 1998). In addition, some have questioned whether resources supporting corridor-based initiatives might be more effectively used in alternative strategies for maintaining landscape connectivity (Simberloff et al. 1992).

Given the relative infrequency of dispersal events and the many difficulties inherent to assessing animal movement across broad scales, studying individual corridor use has been problematic and supporting evidence, by consequence, has been relatively scarce. Assessing the effectiveness of regional wildland networks has been difficult for similar reasons, in addition to the fact that most remain in a limited state of development (Hobbs 1992). The application of complex, spatially explicit models of corridor effectiveness has to some degree been hindered by the paucity of empirical data on dispersal behavior, distances, and the influence of heterogeneity in landcover on dispersal direction (Wennergren et al. 1995). This notwithstanding, there has been some evidence to support the use of corridors for dispersal by some species; this includes documentation of movements through corridors in conjunction with avoidance of adjacent landcover types (Beier 1995; Sutcliffe and Thomas 1996) as well as higher colonization or visitation frequencies recorded for habitat patches connected by corridors as opposed to those that were not (Dunning 1995b; Haas 1995). Although most such evidence comes from observational studies, a few experimental studies have also indicated corridors to have positive effects (Desrochers and Hannon 1997; Haddad 1999). Those who question the corridor approach often do so because of the relative scarcity of empirical evidence in its support and the lack of quantitative studies of dispersal between patches before and after corridor establishment (Vos et al. 2002). Others cite the simplifications inherent in the patch-corridor-matrix model with its emphasis on the structural, rather than the functional, aspects of connectivity and the assumption of an inhospitable, intervening matrix (With and King 1997; With et al. 1997) Similarly, some note metapopulation theory's own tacit simplifications in its use of the patch-corridor-matrix framework (Wiens 1997). Metapopulation models, they contend, may mis-predict functional corridors because they most often exclude such factors as variability in habitat quality within corridors and patches (Rosenberg et al. 1997), the influence of variation in the quality of surrounding landcover (Anderson and Danielson 1997), boundary effects (Wiens 1997), biotic responses to changes in landscape configuration (Hobbs 2002; Yahner and Mahan 2002), and interdependencies in degrees of connectivity across the full range of spatial scales.

If there is any consensus regarding corridors, it may be that they can provide at least some of the answers to imminent problems in conservation planning, depending in particular upon the degree of anthropogenic modification in the landscapes of interest, the spatial scales considered, and the target species or communities of concern (Bennett 1999). Although the creation of linear corridors in substantially human-modified landscapes may not necessarily prove advantageous, protection of naturally existing corridors is likely to benefit biodiversity (Rosenberg et al. 1997). Effective strategies to maintain landscape connectivity, therefore, should include provisions to optimize protection of natural corridors, such as riparian zones, that may already connect suitable habitat core areas (Vos et al. 2002). It is this author's view that corridor-based reserve design may be most appropriate at the regional scale of planning at which: (1) significant fragmentation results from distinctive and high-impact human transportation networks (e.g., highway systems); where (2) landuse patterns mirror those of broad-scale land ownership (e.g., where there exists a positive correlation between agriculture and private land); where (3) ownership patterns reflect broad topographic patterns (e.g., where correlations exist between national forest land and mountain ranges, or between private land and river valleys); and at which (4) extant structural connections between large core protected areas are likely to provide greater potential for transit by multiple far-ranging terrestrial species such as top-carnivores. Even at this scale, however, the potential benefits of corridors should be weighed against or combined with other options to improve connectivity such as creation or restoration of habitat patches, expansion of extant patches, or improvement of habitat quality (Vos et al. 2002).

Spatially explicit methods for predicting, evaluating, and prescribing corridors include vector- and raster-based approaches, as well as static and dynamic models (Dunning et al. 1995a). Prominent among dynamic approaches are individual-based models. IBMs, as such, attempt to predict movement probabilities by way of iteratively simulating the real-time, incremental movement of a hypothetical individual across an "information surface" (often, a grid) weighted according to limiting factors (e.g., security risks), energetic costs (impedances to movement), or predicted habitat quality in the landscape. Simulations are typically run by the Monte Carlo method, whereby cells in the output grid are assigned values in accord with the frequency of their visitation over the iteration set. Linear patterns in the output grid can suggest extant corridors – including possible prescriptions for their enhancement and protection – or they can be used to evaluate other models for corridors. Two closely related kinds of IBMs are Correlated Random Walkers (CRW) and Self-Avoiding Walkers (SAW). CRW models entail rules by which the direction of each move by the modeled individual correlates to some extent with the direction of its preceding move. A variation on CRW, SAW models impose additional constraints to preclude or delay revisitation of previously visited cells.

Least-Cost-Path (LCP) models represent a common, atemporal approach used to inform prescriptions for corridor protections and, indirectly, to assess extant corridors. As with CRW and SAW models, Least-Cost Path models are developed over a cost-surface weighted by resistance to species movement or risk factors. Rather than modeling an individual's progressive encounter of the landscape pattern, however, LCP models adopt a macrocosmic, static perspective on that pattern by which the location and contiguity of individual cells are assessed relative to predefined endpoints denoting habitat patches or core areas. The LCP output identifies the route of least resistance (that is, least-cost) or the highest probability of survival between two endpoints, whereby the "paths" with higher cells values reflect fewer hazards or obstacles, less time in transit, lower total energy costs, or higher-quality habitat (including, for example, more accessible forage or more cover for concealment). Predictions do not concern how an individual might actually negotiate a landscape mosaic in real-time, but rather with what the least-cost route across that landscape would be from a detached and atemporal vantage point. Although LCP models cannot reflect the fine-scale movements of animals, they can provide valid guides for more detailed modeling. Exemplary instances of LCP modeling Walker and Craighead (1997), a study of potential corridors for grizzly bear, cougar, and elk in the Northern Rockies, Bunn et al. (2000), by which interpatch distances for American mink (*Mustela vision*) and prothonotary warblers (*Protonotaria citrea*) were estimated in the Coastal Plain of North Carolina, and Singleton et al. (2002), by which linkages were predicted for sensitive species across Interstate 90 near Snoqualmie Pass, Washington.

Landscape Mosaics and Functional Connectivity

In recent years, researchers have questioned anew the patch-corridor-matrix model's reliance on the premise of discrete landscape elements (i.e., patches and corridors) and dichotomy between habitat and "non-habitat" in the intervening matrix. Functional corridors may not be distinct linear structures connecting patches, but may rather emerge as more diffuse configurations of habitat that facilitate species movement (Gustafson and Gardner 1996; Bennett 1998). Consequent to this, an alternative to the island biogeographic/ metapopulation perspective emerged that has emphasized functional connectivity over that occurring solely by a structural network of patches and corridors. Landscape pattern, by this view, has been re-interpreted more holistically as a complex and continuous mosaic of multiple habitat types (Wiens 1995; Gutzwiller 2002) spanning the entire landscape, matrix included. Patch structure – and by implication, linkages or dispersal potential – arises not from the *a priori* delineation of patches and corridors, but from how and at which scales species relate with landscape heterogeneity (With 1999; Ingegnoli 2002). Thus, by the landscape mosaic view, habitat connectivity is an emergent property of landscapes resulting from the differential interaction of species with landscape pattern (With 1999).

By their very nature, such interactions are as much an expression of the biology and behavioral characteristics of the species concerned as they are of the inherent structural and compositional properties of a landscape. An organism's perceptual and locomotive abilities, energy requirements, and behavioral responses to various landscape configurations may all influence its spatial experience of a landscape and its use of different network patterns in that landscape. Tacitly, questions of scale are also implicated with each of these variables. The perceptual resolution of an animal is defined over a finite range of scales (Kotliar and Wiens 1990), gap-crossing abilities reflect scalar limits to movement, energy needs translate to minimum area requirements, and responses to landscape pattern may vary across scales depending on the scales at which phenomena of interest are manifest (e.g., prey densities, interference competition, broad-scale disturbances, or weather conditions).

Functional connectivity, then, is not only intrinsically species-specific but also highly scale-dependent. From this perspective, a landscape is not intrinsically connected or fragmented; rather, landscape configuration acts as a selective filter, providing passage for some species but not others, depending on their scale-sensitive interactions with landscape pattern (Wiens 1989; With 1994). Thus, underlying the landscape mosaic perspective there is an important requisite – to the extent possible, such approaches must explicitly adopt an organismal or species-centric vantage on landscape pattern (Pearson et al. 1996). Doing so is not only a precursor to assessing functional connectivity; many would also argue (as would this author) that it makes intuitive and ethical sense to avoid viewing landscapes solely in anthropocentric terms.

With the conceptual transition to an emphasis on functional connectivity, the question shifts to the nature of representation within a modeling environment. One answer has come in the form of Neutral Landscape Models (NLMs), maps depicting theoretical landscape patterns as generated through manipulation of various input parameters (With, 1997; With and King 1997). Being "neutral" to the physiographic processes that configure actual landscapes, NLMs provide a null spatial model for quantifying the effects of specific habitat patterns upon connectivity (Gardner et al. 1987; O'Neill et al. 1988; With 1997; With 2002). Within NLMs, measures of habitat connectivity are based, at root, on the abilities (or willingness) of modeled individuals to traverse cells between suitable habitat. An NLM may be based on a presumed dichotomy of "habitat" versus "non-habitat", or modeled gap-crossing abilities may be adjusted to reflect variable habitat quality in the intervening cells. In either case, the species' gap-crossing abilities define the functional adjacencies between suitable habitat cells, and from these connections, patches or clusters of suitable habitat are identified (With 1997; With and King 1997; With 2002). In addition to providing a means of quantifying habitat connectivity based on species-specific movement rules, NLMs can supply insights into the relative importance of habitat abundance (or loss), patch sizes, and gap distances in affecting that connectivity (Andrén 1994).

Conceptually, Neutral Landscape Models are heir to an area of mathematics known as percolation. Based on the study of the flow (or percolation) of liquids through material aggregates, percolation theory has provided grounds for the quantification of connectivity within spatially heterogeneous systems (Stauffer and Aharony 1992). The relevance of this for landscape ecology is clear, where many questions involve the flow of organisms, nutrients, water, or energy through the heterogeneous “aggregates” of landscape mosaics.

Percolation theory has also provided methods (within NLMs) for identifying critical thresholds in connectivity. This is a key idea because habitat is functionally either connected or disconnected, and the shift between these states occurs at a threshold determined by the abundance and spatial configuration of habitat as well as a focal species’ particular movement characteristics (Pearson et al. 1996; With 1997a; Turner et al. 2001; With 2002). The consequences of critical thresholds for conservation are patent given findings that suggest connectivity may be abruptly disrupted as a nonlinear response to habitat loss (With 2002). Incremental loss of suitable habitat may not appear to incur any adverse effects for a focal species until the critical threshold in connectivity is passed, at which point negative effects from fragmentation can become suddenly apparent and the importance of spatial configuration predominant over those of total habitat area (Andrén 1994; Pearson et al. 1996; With 1997a; Turner et al. 2001).

Identification of critical thresholds can provide insights into the nonlinearities between habitat abundance and configuration as they occur across different spatial and temporal scales.

Closely related to percolation thresholds is the concept of the *percolation-* (or, *spanning-*) *cluster*, defined in this context as the structural feature of the modeled landscape that provides for landscape-wide habitat connectivity. Thus, provided a description for the movement capabilities of a focal species (e.g., dispersal distances and gap-crossing abilities), the percolation cluster first emerges in a NLM at the critical threshold in habitat abundance at which continuous species movement is possible across the entire modeled landscape. Conversely, if habitat abundance is assumed constant and the definitions for species movement are varied, researchers can assess landscape-wide connectivity with respect to a range of uncertainty regarding species movement ability, or explore how a landscape may act as a selective filter between species with different movement characteristics.

Neutral Landscape Models are developed on a raster data model, or lattice, and they support analysis of what is often accordingly referred to as lattice-percolation. In recent years several studies have explored habitat connectivity through use of an alternative data model characterized by either bond- or site-percolation known as the graph (Cantwell and Forman 1993; Keitt et al. 1997; Bunn et al. 2000; Urban and Keitt 2001). Graph-theoretic data models are well suited for representing habitat networks in terms of functional linkages as they emerge for a species out of a continuous landscape mosaic. The approach is introduced below, following on that of Bayesian habitat modeling.

Bayesian Habitat Suitability Modeling

Various methods have been applied in identifying suitable habitat for individual target species, including logistic regression (e.g., Mladenoff et al. 1995; Mladenoff and Sickley 1998), multivariate statistical methods (e.g., Clark et al. 1993; Knick and Dyer 1997), and Bayesian rules (e.g., Milne et al. 1989; Pereira and Itami 1991; Aspinall 1992a,b, and 1993).

The use of Bayes theorem to model habitat suitability surfaces requires the assignment of conditional probabilities to specific habitat type associations. Beginning with a set of predictor datasets, conditional probabilities are based on the frequencies of association between each value or class in a predictor dataset and each class (either presence/ absence, or presence/ randomness) in a target distribution (Aspinall 1992b). For mapped data without a temporal component, the frequencies of association correspond with the areas of overlap between each class of a predictor dataset and each defined instance of presence/ randomness. The conditional probabilities for presence (or absence), therefore, are proportionally calculated as the total area of presence (or absence), within each class of a predictor dataset. Alternately, conditional probabilities for the random case are derived from the proportion of the zone of availability overlapping each class of the predictor dataset – the implicit assumption being that distribution is random and therefore in proportion to the study-wide availability of each class in a predictor dataset (Aspinall 1992b).

Once conditional probabilities are assigned to each class of each predictor dataset, the datasets are combined using Bayes theorem:

$$Pp = \frac{pp \ x \prod_{i=1}^{n} cp_i}{pp \ x \prod_{i=1}^{n} cp_i + pa \ x \prod_{i=1}^{n} ca_i}$$

where *pp* = the probability of presence, *pa* = the a priori probability for absence/ randomness, *cp* = the product of conditional probabilities for presence, and *ca* = the product of conditional probabilities for absence/ randomness.

The equation combines the relative and the conditional probabilities for presence versus absence/ randomness. The resulting Bayes output is a single surface comprising a range of probability values that can also be interpreted as relative habitat suitability. For any given location on this surface, the respective cell value represents the probability of presence, or suitability, for that location based on the respective combination of environmental variables in the predictor datasets. Thus, the relationships between a species' distribution and its habitat are intrinsic in the model output (Aspinall 1992b).

As an inductive spatial modeling procedure, advantages to the Bayesian approach are several and are described hereafter (see Discussion). A central assumption for use of the Bayes theorem is the independence of predictor datasets. Although this condition is typically difficult to meet with environmental data, using fewer rather than more predictor datasets can be a means of reducing the potential for error propagation (Aspinall 1992a).

Precedents in GIS-based habitat modeling using Bayes' theorem include studies by Pereira and Itami (1991), Aspinall (1992a, 1992b, 1994), Aspinall and Veitch (1993). Aspinall (1992a) demonstrated use of the Bayesian method by predicting the winter distribution of red deer (*Cervus elaphus*) in the Grampian Region of northeast Scotland. In this study, conditional probabilities were calculated for random subsets of the survey data, with the error bounds thus generated allowing for analysis of error propagation in the combining of predictor datasets through the Bayesian modeling process. To further inform the inductive learning process, the statistical significance of each predictor dataset was also calculated. In a concurrent study in the Grampian region, Aspinall (1992b) generated a predictive surface of curlew (*Numenius* spp) habitat using topographic data derived from a Digital Elevation Model and resampled data from Landsat Thematic Mapper imagery. Here, a threshold based on information content was used (see Forman and Godron 1986) to identify discrete habitat patches in the Bayes output, allowing for subsequent analysis of patch structure, habitat heterogeneity, and curlew abundance using a series of landscape metrics. Aspinall and Veitch (1993) detailed a procedure for classifying a

Landsat TM image directly from wildlife data and elevation data for use as a Bayes model input. By this method, classes in the DEM and the image's spectral values are assigned conditional probabilities using the wildlife presence and absence data. Mean conditional probabilities for each spectral band are then used to combine the image with the DEM using Bayes theorem, providing a predictive map of wildlife occurrence at the full spatial resolution of the satellite image. In a case study demonstrating the applicability of GIS-based spatial analysis for bioclimatic analysis, Aspinall (1994) interpolated climatic data for use as an input to a Bayes model for predicting the distribution of Scots Pine (*Pinus sylvestris*). In developing a predictive model of habitat potential for the Mt. Graham red squirrel, Pereira and Itami (1991) used Bayes theorem in a GISystem to combine two logistic multiple regression models – one built from a set of environmental factors and the other a trend surface based on geographic coordinates.

Graph-Theoretic Habitat Connectivity Modeling

The study of graphs represents a well-established and active subfield of mathematics with a profuse body of supportive literature. In providing a highly versatile framework for understanding network flows, graph theory has seen extensive application across a wide array of fields, including physics (e.g., percolation processes), chemistry (e.g., chemical kinetics), biology (e.g., genetic mapping; molecular evolution), ecology and biogeography (e.g., cladistics), physical and human geography (e.g., stream network and transportation analyses, respectively), information technology and computer science (e.g., circuitry and network optimization), as well as electrical and industrial engineering (Foulds 1992).

In the study of landscape mosaics, graph theory provides an efficient technique for modeling the spatial configuration of actual or potential fluxes of species, energy, or materials among landscape elements. As an early precedent, Cantwell and Forman (1993) sought to identify relatively common and uncommon landscape patterns by comparing graphs based upon mosaics representing a range of climates, dominant landcover and landuse types, and human population densities. Using graphs as the basis for analyses of bond percolation, Keitt et al. (1997) were able to explore critical spatial scales in landscape connectivity, to specify the relative contributions to that overall connectivity made by individual patches, and to assess the importance of landscape pattern to connectivity at different scales. Bunn et al. (2000) used a graph-theoretic framework for quantifying functional habitat connectivity, whereby functional distances between patches were estimated with least-cost path modeling. As a case study illustrating the applicability of the graph-theoretic approach to conservation planning and land management, Urban and Keitt (2001) used graph constructs to address habitat connectivity for the known metapopulation of Mexican Spotted Owl (*Strix occidentalis lucida*).

As is suggestive of its application in many fields, graph theory has accumulated a diverse, and often non-uniform, lexicon (Harary 1969). Similarly, the wide array of questions to which graphs have been applied has generated many kinds of graph operations. For a proper introduction to the formalisms of graph theory and the range of its applications, one can refer to a number of quality texts on the matter (e.g., Foulds 1992; Gross and Yellen 1999, 2004). The following background is inclusive of only those terms and functions that pertain directly to this study's use of graphs. In accord with the review provided by Urban and Keitt (2001), usage here is based primarily upon that in Harary's seminal 1969 text. Because the study of graphs is strongly visual in nature, several figures have also been provided to illustrate the graph terminology described.

Graph Definitions

Any graph G is comprised of *nodes* or *vertices* $V(G)$ and *edges* or *arcs* $E(G)$ such that each edge $e = v_i v_j$ connects nodes v_i and v_j. Any two nodes connected by an edge are *adjacent* to one another, while the edge in-between is *incident* to both nodes (Figure 1). A *walk* is a sequence of adjacent nodes from v_0 to v_n. An *internal* node is a node that is neither initial nor final. *Paths* are walks whereby each internal node is encountered only once. A path's *length* is the sum of the number of its edges. A path is *closed* if the initial node is revisited (i.e., where $v_0 = v_n$), and *open* otherwise. A closed path comprising three or more nodes is a *cycle*. A path without cycles is a *tree*, while a tree that includes every node in a graph is a *spanning tree.* The spanning tree of a graph with the shortest total length is the *minimum spanning tree.*

A graph is termed *connected* if every pair of nodes is joined by a path. A disconnected graph comprises two or more *components* (or, *subgraphs*). Any key node the removal of which disconnects a graph is a *cut-node;* similarly, any edge, the removal of which disconnects a graph, is a *cut-edge* (or, *bridge*).

Connectivity across a graph or component can be summarized using several metrics. The first and most widely known is *vertex-* (or, *node-*) *connectivity* (or, simply, *connectivity*), defined as the minimum number of nodes in a set the removal of which results in a disconnected graph (Oellermann 1996). Noting that this metric is based a "worst-case situation" which may not be indicative of events as they occur across the entirety of a graph, Beineke et al. (2002) introduced *average connectivity*, a global parameter of connectedness that yields the expected number of nodes that must fail in order to disconnect a random pair of nonadjacent nodes. A third measure – one that is inversely correlated with connectivity – is the number of components present. Fourth is a (connected) graph's *diameter* $d(G)$, defined by Harary (1969) as the length of any longest *geodesic*, where a geodesic is a shortest path between nodes i and j. *Diameter* can also be understood as a (connected) graph's maximum *eccentricity*, where the eccentricity of a vertex v is the distance to the vertex farthest from v (Gross and Yellen 2004). A fifth metric, *traversability*, is the longest diameter among any of a graph's components (Harary 1969). And last**,** *circumference*

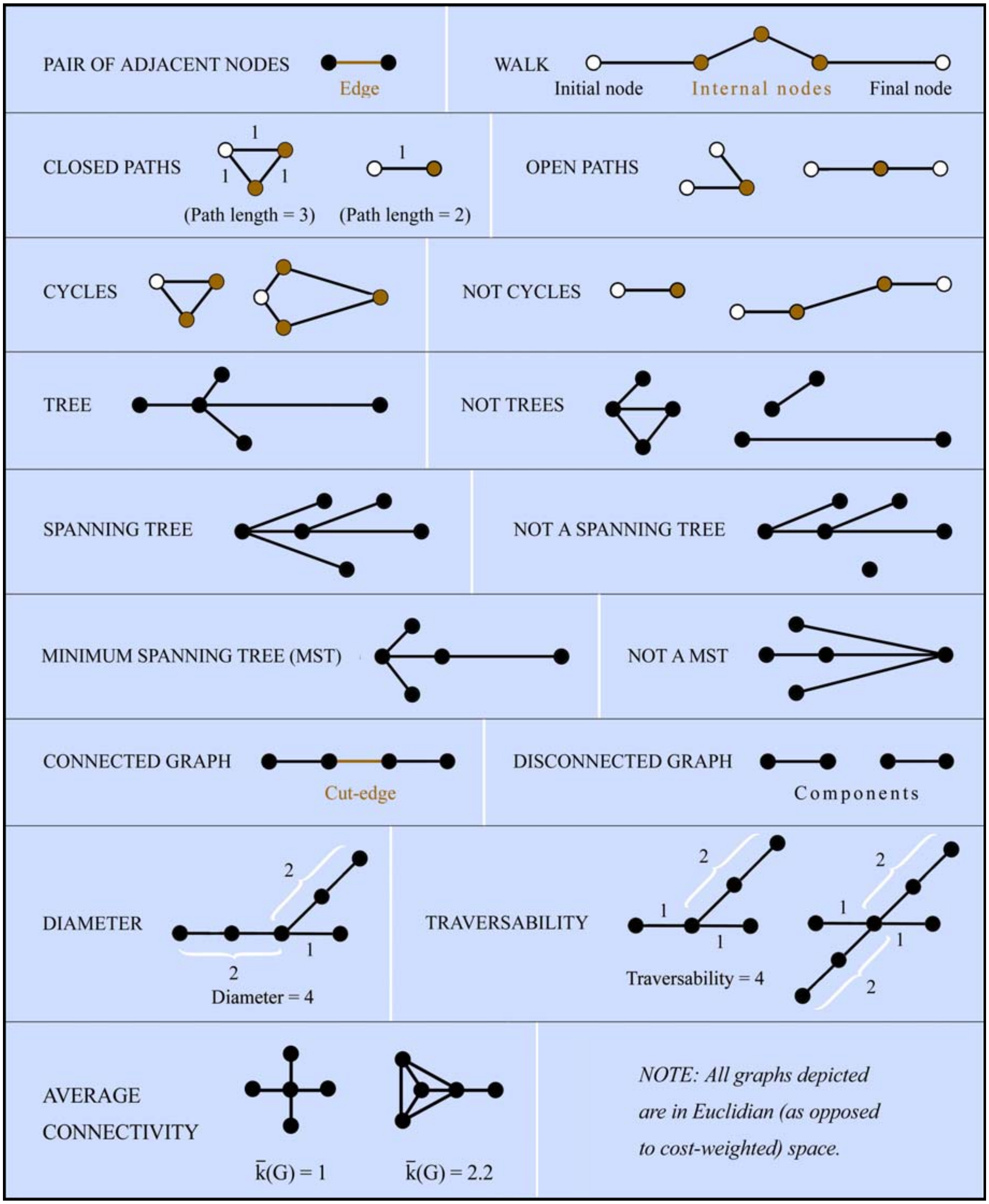


Figure 1 – Graph terminology relevant to this study

c(G), a sixth index, is the length of any longest cycle (Harary 1969). Of these metrics, three were used in this study: number of components, traversability, and average connectivity.

Graph Topologies

In its essence, a graph is determined by its set of connections between nodes. These can be described with a matrix of adjacencies between nodes or conversely with a matrix of incidences between edges. For most applications, an additional array or list is included which summarizes relevant attributes for the nodes as well as their geographic coordinates. Node attributes can be used to modify flow potential through the nodes themselves or to weight flow potential along incident edges.

In this study, nodes were generated as the centroids of habitat patches. Graph topologies were based on adjacencies determined according to one of two alternate definitions for functional interpatch distances. In the first case, distances d_{ij} were measured as the minimum cost-distances between edges[9] (i.e., boundaries) of proximate patches, where cost was defined as impedance to lynx movement in the intervening (interpatch) matrix and patch topology was defined through (cost-weighted) Thiessen polygons. In the second case, distances p_{ij} represented "dispersal probabilities", which expressed the probabilities that a lynx in node *i* would move to node *j*. While many dispersal-distance functions are possible, p_{ij} were derived here as the least-cost distances d_{ij} modified by negative-exponential decay,

$$p_{ij} = - \exp^{(\phi \text{ x } d_{ij})}$$

where ϕ was a distance-decay coefficient ($\phi > 0.0$).

Depending on the species of concern and the degree to which patches have been resolved, it may be appropriate to weight distances d_{ij} or p_{ij} by potential node attributes such as the area or relative quality of habitat patches they represent. Distances d_{ij} weighted by patch areas would lead to a *gravity model*, whereas distances p_{ij} weighted by factors influencing the likelihood of patches to as act sources (e.g., patch area, habitat quality, or population densities) would constitute an index of *dispersal flux*. Area-weighted cost distances and dispersal fluxes were excluded from this study for two related reasons. First, patch edges (and, by implication, patch areas) were not considered to be of sufficient distinction to support area-weighted distances; second, patches, as defined, were not large enough to function as "source areas" in terms of metapopulation structure and dynamics.

Graph Representations of Significant Linkages

Beyond measuring global connectivity, this study identified important habitat linkages based on derivation of minimum spanning trees and identification of cut-edges. Minimum spanning trees were found for graphs with topologies based on cost-weighted distances d_{ij} and alternately for those with topologies based on dispersal probabilities p_{ij}. Because a graph can contain only one minimum spanning tree and this tree is predetermined by the graph's topology, it can be generated directly for any graph without any additional requisite graph operation. Cut-edges were found only for graphs based on cost-weighted distances d_{ij}.

Because, in this study, cut-edges were not necessarily extant in initial graphs, their identification (i.e., as the weakest links in habitat patch networks) involved the systematic removal of edges from the initial graphs based on specified interpatch distances – a graph operation known as *edge-thresholding*.[10]

Graph Interpretation

When used to model connectivity within landscape mosaics, it should be understood that graphs and graph constructs exist in a quasi-conceptual space that is anchored to actual geographic space only through the coordinates of nodes and that these locations are simplifications in themselves of the entities they represent. By implication, the locations and orientations of edges, as well, only approximate those of the actual landscape features and functional connections they represent. This correspondence is, of course, critical to the task of using graphs to identify those areas in a landscape that bring about functional habitat connectivity. In cases where the relative distinction and isolation of habitat patches approaches that of the island-biogeographic model (e.g, at the scale of regional metapopulation structures), the effects of edge displacement from the geographic features they represent may well be nominal for interpretative purposes. However, even in cases – as in this study – where habitat patches are less resolved and relatively near to one another, a practical sense of the degree of this correspondence can be realized given consideration of the spatial grain and extent of the underlying patch surface as well as node densities in the graph; edges between clustered nodes, that is, will have stronger correlations with the features they represent than will those between diffuse nodes. For studies using graphs to model open systems, a key ramification is that recognition of these spatially explicit "edge-feature" (or, "edge-process") associations relies on visual interpretation of the graphs.

Graphs by their very nature invite both quantitative and visual interpretation. While .numerous metrics (e.g., *order*, *diameter)*, and graph-theoretic concepts (e.g., *traversability*, *planarity*, *coverings*) exist to support quantitative characterization of graphs and their properties, graphs themselves and various graph constructs (e.g., *spanning trees*, *Hamiltonian cycles*) also support inferential understanding and visual pattern recognition.

CASE STUDY

Study Area and Location Data

From October of 1981 through February of 1988, two successive lynx studies (Brittell et al. 1989, and Koehler 1990) were conducted in a 1,795 km^2 area of north-central Washington (48°15′ to 49°N, 119°45′ to 120°15′W).

The study area covers much of a subalpine plateau, the Okanogan Highlands, located on the eastern side of the northern Cascade Range (Figure 2).

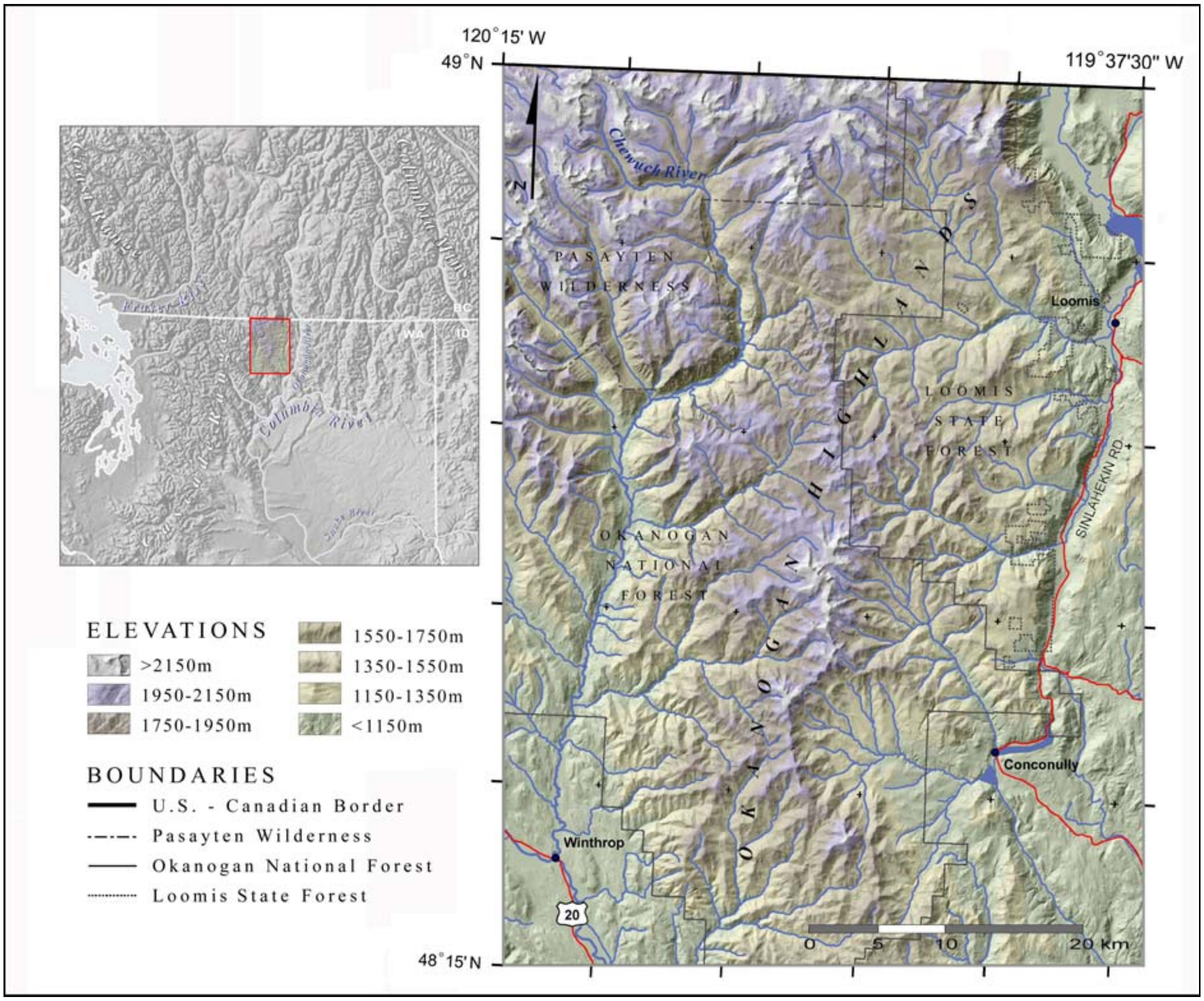


Figure 2 – The Okanogan Highlands

While volcanic activity and glaciation have resulted in relatively steep slopes east of the range (McNab and Avers 1994), more gentle, rolling terrain predominates over the plateau itself, with 86% of slopes within the study area below 30°. Elevations within the study area range from 750 to 2540 m (McKelvey et al. 2000c). Soils are primarily andisols, owing to volcanic ash originally covering the eastern slopes (McNab and Avers 1994).

In the rainshadow of the northern Cascades, the study area's localized climate is distinctly subalpine, with generally more insolation, greater diurnal temperature fluctuations, and warmer peaks than in the boreal climates of the taiga (Agee 2000). Through the duration of Koehler's (1990) study, daily temperatures ranged from -23 to 35°C and mean annual precipitation was 51 cm at 660 m elevation (National Oceanic and Atmospheric Administration).

Major forest associations include Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) at elevations below 1370m and on southerly aspects at higher elevations. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant associations at higher elevations, and lodgepole pine (*Pinus contorta*) and aspen (*Populus termuloides*) the dominant seral tree species (Williams and Lillybridge 1983).

Most of the study area falls within the Okanogan National Forest and the adjacent Loomis State Forest. Immediately to the northwest is the Pasayten Wilderness and to the north, British Columbia and the continuation of the plateau.

Movements of radio-collared lynx were monitored at 7- to 15-day intervals from the air and at 1- to 7-day intervals from the ground, cumulatively resulting in 842 radiolocations over seven years for 9 adult females and 13 adult males (Koehler 1990).[11] During snowtracking, lynx were approached to within 200 m. Locations were plotted to the nearest 50m on 1:62,500 USGS topographic maps. Estimated telemetry error averaged 200 m for locations obtained from 1982 through 1986 (Koehler 1990), though it was not estimated for other years (McKelvey et al. 2000c).

In addition to collecting lynx data, Koehler counted snowshoe hare pellet counts within ten, 1 m radius circular plots spaced at 10 m intervals along each of 63 transects. Associated attribute data included UTM locations of transects as well as habitat type, stand age, overstory, elevation, slope, aspect, and dates recorded by sample plot. Snowshoe hare tracks were also counted along the transects during winter.

Lynx Ecology

The determination a set of candidate predictor datasets for the Bayesian models relied on a review of the available literature on lynx ecology. In justifying the selection of predictor variables for lynx in southern populations, we can begin with what is known of lynx ecology across their entire range.

Continental and Regional Distributions

At a continental scale, Canada lynx are known to occur in boreal, sub-boreal, and mesic western montane forests that experience relatively cold, snowy winters and support a sufficient prey base of snowshoe hare (Ruggiero et al. 2000b). Regional lynx distributions are also thought to be influenced by snowshoe hare distribution, snow conditions, and vegetation cover types and structure (Ruggiero et al. 2000b). Of these, vegetation type is the easiest to classify from remote sensing imagery and, consequently, it has been used most prevalently to predict lynx distributions at broad scales. Limited evidence for the Western U.S. suggests that lynx are associated with those mesic forest types which – as southern extensions of boreal forests – are dominated by lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and, occasionally, aspen (*Populous tremuloides*) cover types (Ruggiero et al. 2000b). Mesic Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), or western larch (*Larix occidentalis*) stands, where they are interspersed subalpine forests, are also known to provide lynx habitat (Koehler 1990; Koehler and Brittell 1990; Koehler and Aubry 1994; Agee 2000; Mowat et al. 2000; McKelvey et al. 2000b,), as occasionally can Pacific silver fir (*Abies amabilis*), western red cedar (*Thuja plicata*), western and mountain hemlock (*Tsuga heterophylla* and *Tsuga mertensiana*), riparian shrub habitats (e.g., alder, *Alnus* spp., and willow, *Salix*, spp.), and shrub-steppe habitats (USFWS 2001).

Predictor Variables at Subregional Scales

Snowshoe hare distribution, snow conditions, and vegetation type and structure are also thought to influence lynx distributions at subregional scales. Topography and canopy closure, as well, may be important at these finer scales. Collectively, it is these variables that were reviewed as potential candidate predictor variables for this study.

Snowshoe Hare Distributions. Lynx distributions at subregional scales may be strongly influenced by their ecological relationship with snowshoe hares. Snowshoe hares are the primary prey species of lynx across their range (Koehler and Aubry 1994) .[12] As a result, lynx density, home range size, dispersal patterns, reproductive parameters, and survival rates are strongly correlated to snowshoe hare abundance (Ward and Krebs 1985; Breitenmoser and Slough 1993; Poole 1997a). In the Highlands study area itself, Koehler (1990) noted that lynx preyed primarily on hare, while both McKelvey et al. (2000c) and Aubry et al. (2004) found that lynx occurrence was correlated with higher hare densities.

Estimated hare densities, then, should constitute an exceptional predictor of lynx presence. However, hare data collected by Koehler (1990) were neither considered representative by McKelvey et al. (2000c) nor of sufficient spatial resolution to support interpolation of an accurate, study-wide predictive surface for hare densities. That said, the analysis of hare use of forest cover types did prove instructive in this study by guiding the reclassification of the original species group layer (see Appendix B). Many of the revised classes in the "plant series" layer proved capable of discriminating between lynx presence and randomness, suggesting that, in combination with other predictors such as stand structure, the plant series layer is worthy as a practicable surrogate for hare densities.

In general, this study addressed the influence of snowshoe hares on lynx distribution by basing the selection of candidate predictors in part upon a concomitant review of literature on hare habitat selection. The rationale for this is simple — because lynx are co-adapted with snowshoe hare, they may often select for those habitat characteristics preferred by hare.

Snow Conditions. Lynx distributions at subregional scales may be related to snow conditions in several ways.

First, by virtue of their proportionally large feet and low foot loading, lynx are widely believed to benefit from a motive advantage in deep snowpacks over potential competitor species such as cougar (*Felis concolor*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). Although Aubry et al. (2004) found that lynx selected for firm snow over two winters, it is unknown whether or not lynx actively select for snow depth (or, softer snowpacks in other instances). More evident is an avoidance of deep snow by cougar, coyotes, and bobcats. Under "normal" winter conditions (and notwithstanding increased access snowmobile trails provide to generalist predators), this is thought to result, generally, in spatial segregation of these species from lynx, as was determined to be the case with coyotes by Murray and Boutin (1991) and Litvaitis (1992). Although exploitative competition is unlikely to significantly impact lynx where it is overwhelmed by cyclic changes in hare availability, interference competition may be an important factor affecting lynx numbers (Buskirk et al. 2000) and spatial displacement of the latter may promote greater lynx abundance in areas which experience deeper snowpacks.

Second, snow depths may directly influence selection behavior of some adult female lynx — those with kittens may at times select for areas that provide thermal cover under exposed woody debris.[13]

Third, variable snow depths affect lynx by causing a vertical shifting of foraging platforms used by snowshoe hare. Combined with the patchiness of vegetation cover, this fluctuation results in lateral spatial displacement of hare distributions throughout the year.

Accordingly, an early exploratory effort was made to develop a predictive surface for snow depth across the study area. Monthly point measurements of snow depth and of Snow Water Equivalent (SWE) were averaged, respectively, at each of 29 proximate snow courses across the seven years of the two telemetry studies, then interpolated into two respective predictive surfaces using ordinary kriging.[14] Results, however, confirmed that there were insufficient snow courses in the area to support predictive surfaces capable of discriminating study-wide habitat selection patterns.

Topography and Forest Cover. While the spatial resolution of available data precluded use of snowshoe hare densities and snow depths as candidate predictors of lynx presence, sufficient data does exist for the six topographic and forest cover variables that follow. In part serving as surrogate variables for hare densities and snow depths, these were chosen in accord with evidence in the literature supporting their influence on habitat selection at subregional scales by either lynx or snowshoe hares.

Elevation. Across their range, elevations of lynx habitats vary, depending on moisture patterns and temperature regimes (Ruggiero et al. 2000a). However, when considered at subregional scales, elevation can be considered predictive of lynx habitat by virtue that it correlates with several variables believed to be important to lynx habitat selection, including vegetation cover types, snow depths, temperature regimes, and the history and nature of anthropogenic changes in landcover composition and configuration. In the case of vegetation cover, for instance, western montane forests with boreal characteristics generally occur across Washington at elevations above 1,400 m (Agee and Kertis 1987), while proximate to the study area on the eastern slopes of the Cascade Mountains, subalpine fir plant associations that provide for primary lynx habitat (Koehler 1990, Apps 2000, McKelvey et al. 2000b) are generally present only above 1220 m (Williams and Lillybridge 1983, Lillybridge et al. 1995).

Suggestive of the general covariance between elevation and snow depth, significant seasonal shifts in elevation use by lynx were detected in the North Cascades study area by McKelvey et al. (2000c) and in the southern Canadian Rockies by Apps (2000). Differential seasonal elevation use, in these cases, may occur either as a result of selection by lynx of deeper snowcover so as to reduce interference or exploitative competition from other carnivores, as suggested by Apps (2000), or indirectly as a result of the changing distributions of snowshoe hare in response to fluctuating seasonal feeding platforms of exposed (above-snow) browse. By virtue of such correlations, elevation can provide a useful surrogate for these variables; moreover, in the capacity of supplementing layers classified from satellite imagery, elevation datasets provide the notable advantages of objective generation, relatively high spatial resolution, and quantifiable error estimates.

<u>Slope.</u> Although relatively few studies have reported on selection patterns for slope by lynx, what data exists suggests that some individuals may prefer flatter terrain during periods of snowcover. Using logistic regression techniques, McKelvey et al. (2000c) detected significant selection for flatter slopes during winter by lynx in the North Cascades population, while in the southern Canadian Rockies, Apps (2000) found that a majority of radio-collared lynx avoided or

did not select steeper (> 40%) slopes and either preferred or did not avoid more moderate slopes (< 40%).

Closely related to slope is the concept of topographical complexity (or, terrain ruggedness), which serves as a metric for the extent of variation in relief of the landscape.[15] Apps (2000) and McKelvey et al. (2000c) have each indicated that lynx appear to prefer gentle terrain when it is available, while Koehler and Aubry (1994) have noted that in mountainous terrain, lynx exhibit a propensity to occupy "benches, plateaux, valleys, and gently rolling ridgetops." Although these observations come from studies conducted within or proximate to the Highlands study area, topographical complexity, as such, was not chosen as a candidate predictor for this study. Rather, the use of both slope and aspect was deemed sufficient to address lynx selection for conditions of terrain relief.

Aspect. Lynx selection for aspect is widely believed to occur in response to the need for thermoregulation or as an artifact of covariation with selection for certain snow conditions (i.e., whereby slopes with northeastern aspects are typically wetter and cooler than those with southwestern aspects). In either case, selection for aspect may prove difficult to detect as it may occur at spatial scales finer than the error associated with many telemetry locations. Moreover, if and when fine-selection for aspect is prompted by thermoregulatory needs, its detection may be further confounded by high daily and weekly fluctuations in insolation at these scales (Apps 2000). In spite of these complications, however, McKelvey et al. (2000c) detected a preference for northeast aspects by lynx in the Highlands study area. For the same population, Koehler (1990) documented all denning sites to occur on north-northeast aspects — evidence suggesting that thermoregulation may be important during denning activity.

Stand Structure. The structural characteristics of a forest stand are believed to strongly influence snowshoe hare abundance and, thus, to affect lynx foraging activity. Hares rely on low, woody vegetation that composes a relatively dense horizontal structure through a stand's understory — conditions which provide accessible browse and refugia from predation. (Litvaitis et al. 1985; Hodges 2000a). Specifically, hares prefer stands that are well-stocked, those at ages at which branches provide more lateral cover, and those that contain relatively high densities of small-diameter stems or twigs (Litvaitis et al. 1985; Koehler 1990; Hodges 2000a). Dense, multi-layered understories are especially suitable, as they provide forage and cover as the hare's feeding platform varies in height with fluctuating snow depths (Litvaitis et al. 1985; Koehler 1990 and 1991). Documenting a broad consensus among snowshoe hare studies from across their range, Hodges (2000a) noted that, more specifically, hare densities across different (range-wide) habitat types were higher in understories with cover ranging from approximately 1 to 3 m.

Lynx denning activity also appears to rely on certain structural characteristics, namely the presence of coarse woody debris, such as downed logs or root wads, which provide protective escape and thermal cover for kittens (Koehler 1990; Mowat et al. 2000; Squires and Laurion 2000). Koehler (1990) found dens in the Highlands study area to be located within an average density of 40 downfall logs per 50 m^2.

In that different seral stages will exhibit characteristic structural features, it is meaningful to a discussion of structure to also consider stand age class. Several studies have indicated that stand ages which contain greater lateral cover are more heavily used by snowshoe hares (Wolfe et al. 1982; Litvaitis et al. 1985). Early seral stands, in particular, may support higher densities of snowshoe hare than more mature stands (Byrne 1998), a finding corroborated by Koehler (1990) to be the case in the Highlands study area. It follows that early-successional stands may also tend to exhibit the highest potential as lynx foraging habitat (Koehler and Aubry 1994; Mowat et al.

2000). However, with reference to range-wide lynx foraging success, Ruggiero et al. (2000b) concluded that no single class appears to be critical in composing hare habitat or contributing to hare productivity, as various successional processes and scales of natural disturbance may be responsible for the emergence of the structural conditions required by hare in the understory. Thus, whereas ephemeral, regenerating stands have been associated with high hare densities, temporally stable late-seral forests have also been found to be moderately productive for hares (Murray et al. 1994; Buskirk et al. 2000). In seeking dense cover and accessible browse, hares may select for different seral stages depending upon specific cover species, localized successional history, and current snow depths (Hodges 2000a*)*.

In contrast to the dense understories characterizing productive snowshoe hare habitat, the coarse woody debris associated with lynx natal dens has a more consistent age class signature. Koehler (1990) and Poole (1997a) found dens to be located within older regenerating stands (> 20 years since disturbance) or in mature conifer or mixed conifer/ deciduous forests.

In summary, to the extent that age class is indicative of stand structure, optimal lynx foraging and denning habitats are represented by opposite ends of the sere. In light of this**,** Ruggiero et al. (2000b) concluded that lynx persistence relies on a range and mosaic of stand ages and furthermore that the degree of interspersion between early- and late-successional stands need be such as to provide that foraging habitat is “nearly adjacent” to denning habitat. Habitat interspersion may also benefit snowshoe hares by providing them with continual access to browse and protective cover even as variable snow depths alter the feeding platform.

<u>Species Group.</u> Effectively synonymous in this case with plant series, species group was chosen as a predictor primarily as a means to discriminate lodgepole pine stands. Whether occurring as the dominant species within a plant association or occurring intermingled within larger stands of subalpine fir or Englemann spruce, there is considerable evidence to indicate that

seral lodgepole pine is of principal importance to quality snowshoe hare and lynx habitat in western Montana and north-central Washington. Multiple studies documented in Ruggiero et al. (2000a) showed that lodgepole pine was one of the primary forest types in use by snowshoe hares in Montana, Colorado, Washington, and Utah. In the Highlands study area where hardwood browse was not available, Koehler (1990) reported that snowshoe hare pellet densities were greatest in lodgepole pine types and that hares fed almost exclusively on lodgepole pine seedlings. Koehler (1990) and Hodges (2000b) both showed that younger stands of lodgepole pine (20-25 years old), specifically, had the highest hare densities in this area. Based on known locations of lynx, Koehler (1990) reported that minimum convex polygon (MCP) home ranges contained a higher proportion of lodgepole pine and a lower proportion of Douglas-fir types than did the entire study area. Also, in their reanalysis of the combined data from Koehler (1990) and Brittell et al. (1989), McKelvey et al.(2000c) found that lynx showed strong selection for lodgepole pine during winter, with use of all other forest cover types =< 15%. In a prior study in western Montana, Koehler et al. (1979) found that radio-tracked lynx used densely stocked stands of lodgepole pine nearly exclusively.

Recent arguments by USFWS (2001) and Mowat et al. (2000) have maintained that stand structure is more important to snowshoe hare and lynx habitat than is species composition, and, moreover, that the apparent influence of particular species types is primarily a consequence of their predominant physical nature (structural variation by age class notwithstanding). This contention draws support from the fact that, within the boreal, sub-boreal, or mesic western montane forest types where they occur, lynx are known to inhabit different plant series at finer scales. Similarly for snowshoe hares, Hodges (2000b) indicated that no given tree species is inherently more important than another, reporting that hare use is more closely correlated with the structural component of a stand’s understory than its species composition.

The significance of seral lodgepole pine for lynx and snowshoe habitat in western Montana and north-central Washington appears to be due to the understory structure typical of such stands. As well as being relatively short-lived, lodgepole pine is highly susceptible to such natural disturbance processes as wind, fire, and insect outbreaks. These characteristics are conducive to more frequent stand-replacement events, which provide for both the relatively dense understory cover and high stem densities valuable to hare (Agee 2000) and more abundant coarse woody debris of importance for lynx denning activity.

In sum, classification of lodgepole pine was considered important to this study as an auxiliary strategy by which to represent stands that are likely to exhibit structural characteristics most suitable for hare browsing and lynx denning. Species group was chosen as a complement to the stand structure predictor variable for this reason, as well as out the recognition that, in most cases, plant series is easier to classify reliably from satellite imagery.

<u>Canopy Coverage.</u> During exploratory and dispersal movements lynx have been known to travel across considerable distances with relatively sparse vegetation cover (e.g., shrub-steppe habitats). However, there is evidence to suggest that resident lynx avoid crossing areas of little or no canopy coverage, particularly while hunting. Monitored lynx in the Highlands study area preferred moving through continuous forest cover, and snow tracking indicated that individuals were unlikely to cross openings of > 100 m (Koehler 1990). Aubry et al. (2004) also found that lynx avoided meadows and areas of recent timber harvest.

Such avoidance of large openings may be related to snowshoe hare distribution. Hares in the Highlands study area avoided clearcuts and very young stands (Koehler 1990), while overstory trees are believed to benefit hares through reduced snow accumulation and greater exposure of understory vegetation (Hodges 2000b). Thus, avoidance of openings by lynx may be a response to the limited use by hare of areas lacking in above snow cover, as suggested by Mowat et al. (2000).

Predictor Data

To summarize, review of the literature on lynx and snowshoe hare ecology provided justification for use of the following six candidate predictor variables: elevation, slope, aspect, stand structure, species group, and canopy coverage. Datasets for the topographic variables were derived from a seamless, level-2, 10 m Digital Elevation Model acquired from the USGS National Elevation Dataset. Datasets for the landcover variables were derived from classifications (cell-size 25 m) of several Landsat images (dating from the early to mid-1980s) conducted for the Okanogan National Forest by Pacific Meridian Resources, Inc. (PMR).

METHODS

Framing Habitat Selection

Any analysis of wildlife habitat selection requires definitions for: (1) habitat types, (2) the zone(s) of potential habitat available to the sampled population, and (3) presence versus absence of individuals in that population (where, provisionally, a random distribution may be substituted for known absence). In this study, the topographic and landcover datasets provided the classifications for different habitat types, zones of availability and lynx presence were each determined from telemetry locations, and a randomized distribution was used as a substitute for known absence.

Reclassification of Predictor Data

Several versions of each original predictor dataset were prepared, each with increasingly broad class intervals (see Appendices B and C). Where possible, class breaks were chosen to reflect distinctions believed to be most relevant to selection behavior by the radio-collared lynx as discussed by Koehler (1990). With each reclass, it was necessary that the number of resulting classes were few enough to enable valid tests of association for a majority of classes while remaining numerous enough to provide for delineation of meaningful ecological distinctions. Class breaks for the first reclass of the elevation layer were set at 100 m intervals, with those in each successive version increased by 50 m. Successive revisions of the slope dataset were reclassed at intervals of 10°, 15°, and 30°. To more effectively capture general distinctions in temperature and moisture gradients, aspect was transformed from a radial statistic into a measure of angular distance from the northeast (after McKelvey et al. 2000c). Redefined aspect values thus ranged from 0° on the colder, wetter slopes due northeast to 180° on warmer and drier slopes to the southwest, with flat areas assigned a value of 180° due to their relatively high levels of insolation. One reclass was made for each of the three original landcover datasets. First, stand size was simplified to six classes while maintaining a range across stand ages. Second, species group was revised into classes defined principally by plant association (Williams and Lillybridge 1983), the sole exception being the designation of a new class to include any of the original forest cover classes that were either fully or partially composed of substantial lodgepole pine stands. This class (PICO) was defined as such in response to Koehler's (1990) findings of strong evidence for the predominant selection by snowshoe hares of ~20-year old lodgepole pine stands and secondary selection of older lodgepole pine cover. Third, canopy coverage was simplified to three classes based on closure percentages.

Selection Scenarios

Analyses of habitat selection were framed in accord with three alternative strategies, each resulting in a set of Bayes models and an eventual aggregate habitat suitability surface. The first two approaches addressed scale-specific selection behavior and individual variability. Both entailed multi-scalar selection analysis for each individual in a subset of the lynx population. They differed, however, in the means by which individual home ranges were defined and in the number of individuals considered. The third approach addressed seasonal habitat selection at a single scale of analysis, using locations pooled across all 22 lynx.

Scenarios One and Two. Selection by individual lynx was examined at each of two biologically based spatial scales (sensu Johnson 1980). In this study, "meso-scale selection" refers to that by an individual of its home range from within the meso-scale zone of availability, an area of shared importance to the lynx population (i.e., Johnson's second-order selection). In contrast, "fine-scale selection" refers to that by an individual of certain habitat components from within its own home range (i.e., Johnson's third-order selection).

Meso-scale Availability and Lynx Presence. Definition of the meso-scale zone of habitat availability required an initial delineation of the study area; this was characterized as the 100% minimum convex polygon around the 842 locations of the 22 lynx, buffered by the diameter (4.8 km) of the average 50% adaptive kernal home range (after McKelvey et al. 2000c). To demarcate the meso-scale zone of availability, elevation zones of < 1350 m and > 2150 m were then removed, as well as non-contiguous, outlying areas, reducing the available area by 23.5% yet leaving 98.9% of the locations ($n = 833$ for 22 lynx) (Figure 3).

Meso-scale lynx presence was defined for each individual as an estimate of its home range. Two home range estimators were used, the Jennrich-Turner method (Jennrich and Turner 1969) and the fixed kernal method (Worton 1989). Both methods are in common use by ecologists, yet each differs in its accuracy, bias, and requisite assumptions made of location data (White and Garrott 1990). The Jennrich-Turner method is notable for its lack of sensitivity to lower sample sizes (White and Garrott 1990) and because it provides an estimate of precision. Its principal disadvantage lies in its assumption of an underlying bivariate normal probability distribution to an animal's locations, which is to say that the individual moves randomly about a central locus of activity — an assumption that has led to claims that the method often oversimplifies an animal's pattern of spatial use (Kie et al. 1996). The fixed kernal method, in contrast, has the advantages of being free of parametric assumptions and having well studied, consistent statistical properties (Worton 1989). However, kernal methods also entail lower precision and a higher sensitivity to sample size in comparison with the Jennrich-Turner estimator. To assure reliable home range

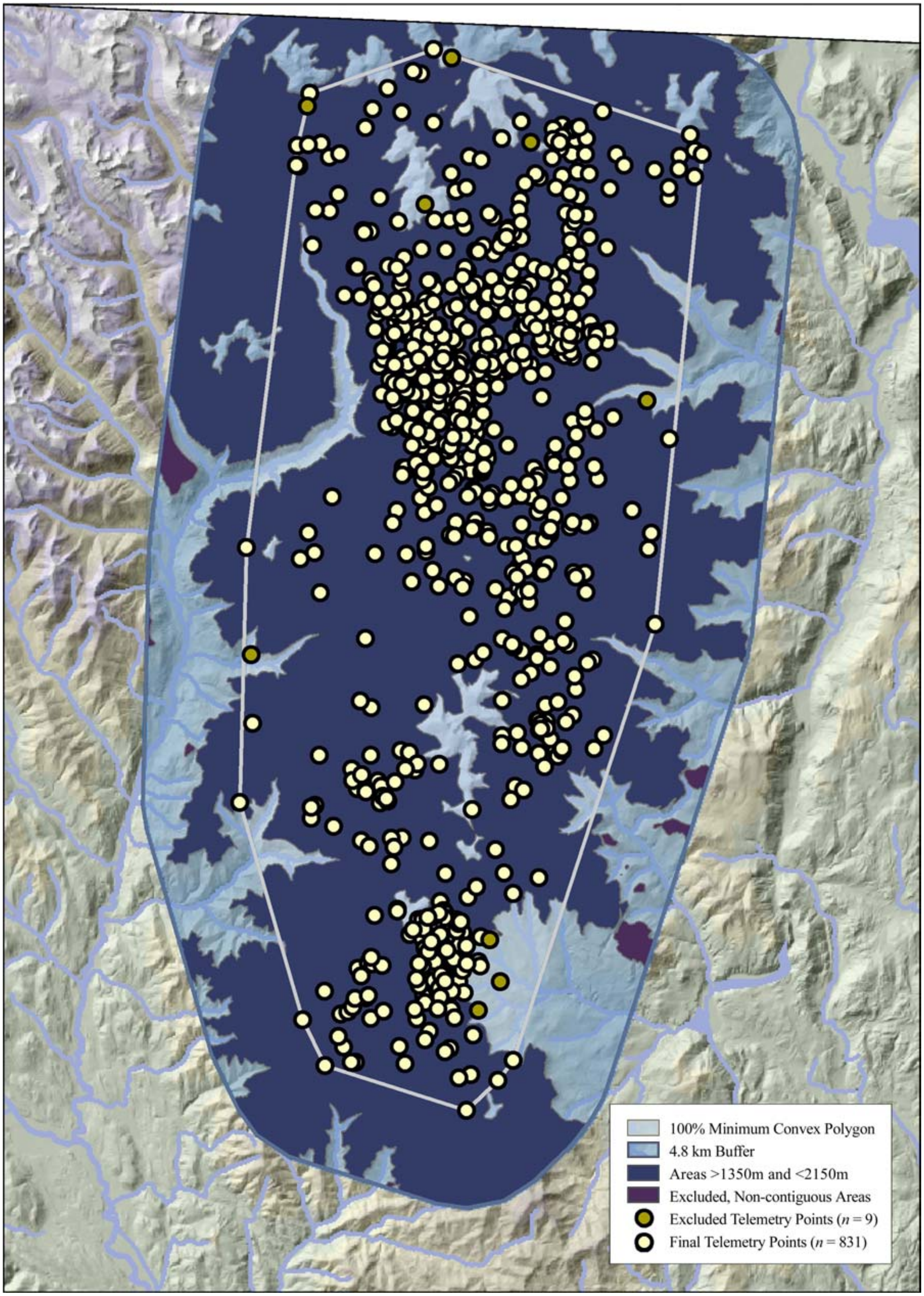


Figure 3 – Definition of the meso-scale zone of availability

estimates, use of the Jennrich-Turner method is generally recommended only where n >= 40 locations, and that of the fixed kernal estimator only where n >= 50 locations (White and Garrott 1990).

Both methods were applied using the Animal Movement Extension for ArcView (Hooge and Eichenlaub 1997) and compared through their respective use in the first and second selection scenarios. The Jennrich-Turner estimator was used for the ten lynx for which n >= 39 (Figure 4a), while the fixed kernal estimator was used for the five lynx for which n >= 49 (Figure 4b). Boundaries of Jennrich-Turner home ranges were designated at the 90% probability ellipse. Those of fixed kernal home ranges, generated using Least-Squares Cross Validation (LSCV) as a smoothing factor, were similarly set at the 90% probability polygon.

Fine-scale Availability and Lynx Presence. In addition to providing definitions of lynx presence for the meso-scale analyses, home range estimates were used to define available habitat for fine-selection by individual lynx. Definition of fine-scale lynx presence was based directly on individual radiolocations. Because an average error of 200 m was estimated for the telemetry (McKelvey et al. 2000c), buffers with 200 m radii were applied to the point locations, then rasterized. Resulting areas (rather than counts) were regarded as the measure of frequency to represent fine-scale lynx presence. This approach not only addresses locational uncertainty in the telemetry, but also mitigates for the effects of relatively small sample sizes in the model (Aspinall 1994).

Scenario Three. The third selection scenario focused on possible seasonal differences in habitat selection patterns at the meso-scale zone of availability (Figure 4c). Because relatively low representation of individual lynx precluded season-specific subsampling by individual, locations

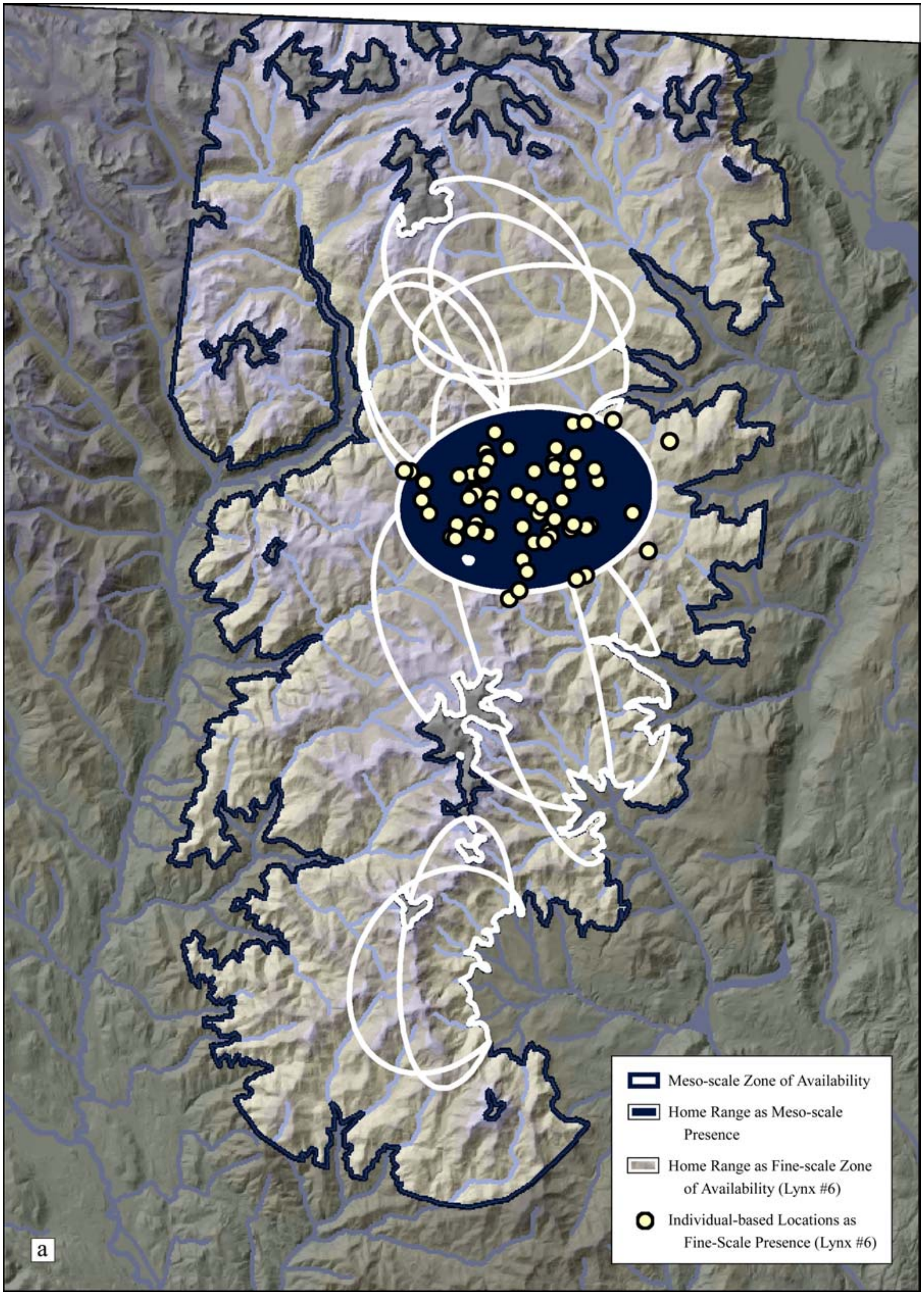


Figure 4a – Selection Scenario One: The Jennrich-Turner method

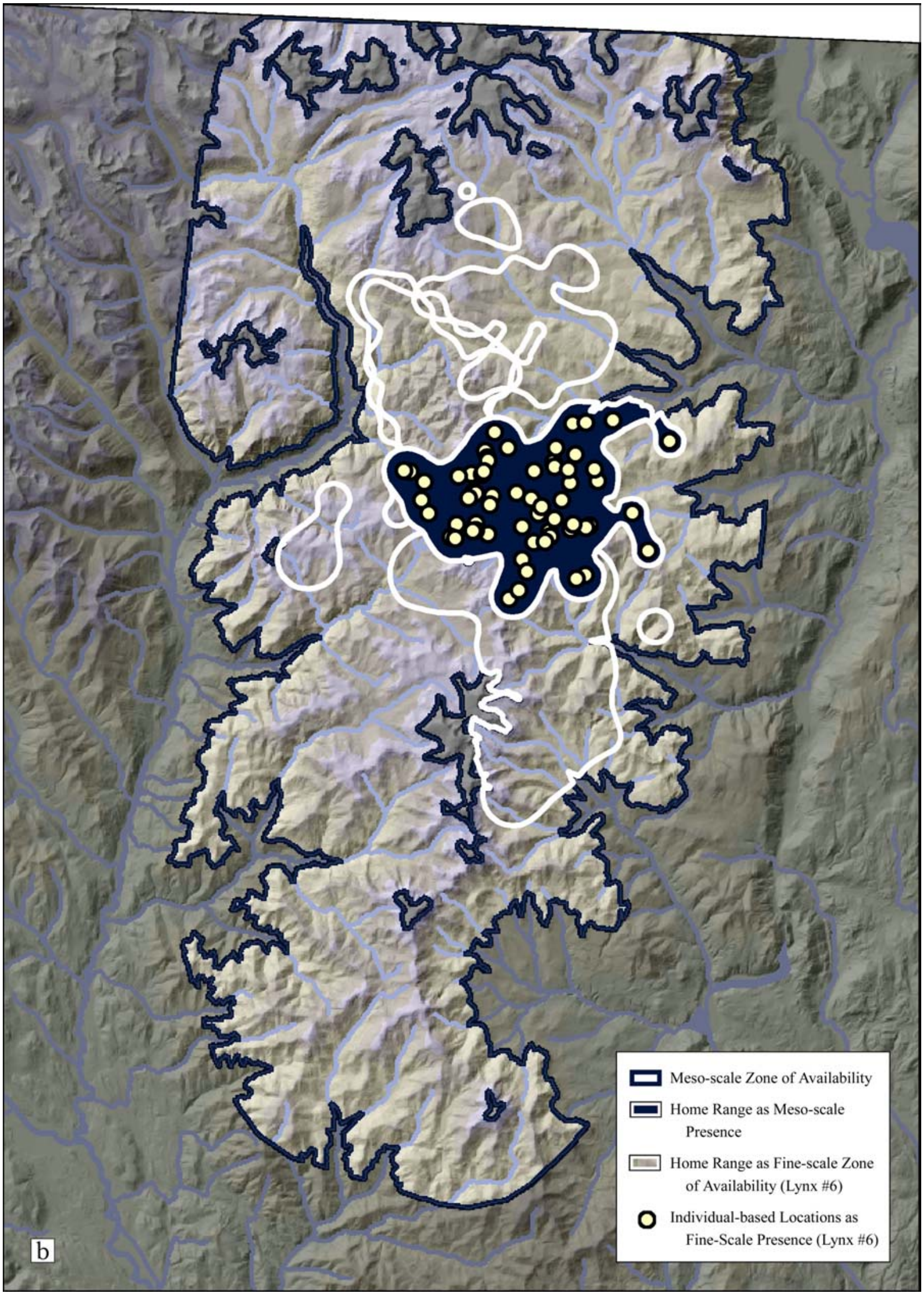


Figure 4b – Selection Scenario Two: The fixed kernal method

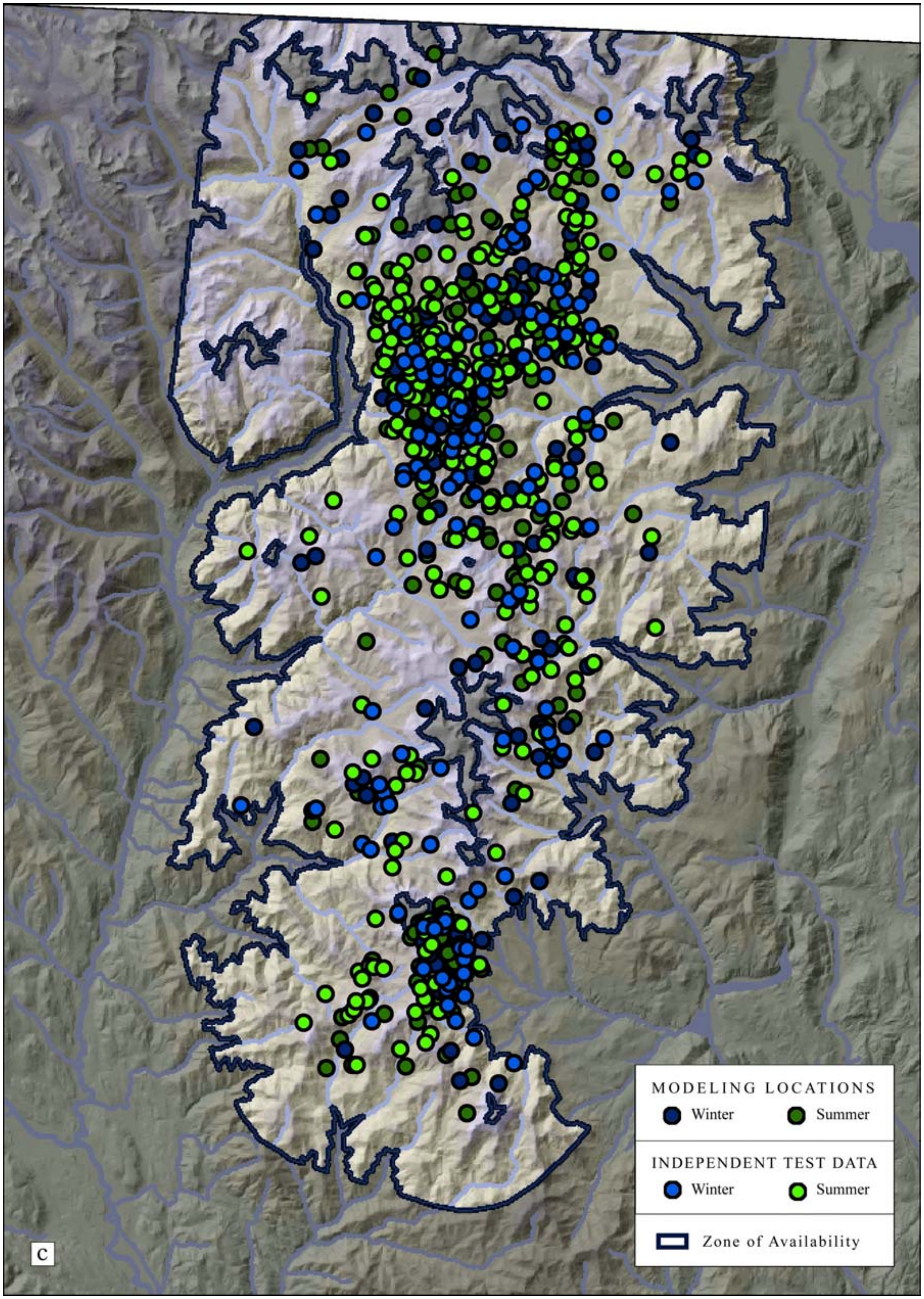


Figure 4c – Selection Scenario Three: Single-scale, by season were pooled across all 22 lynx (*n* = 833 after removal of 9 points falling < 1350 m or > 2150 m), then split by season. A functional distinction between "winter" and "summer" was developed with respect to the possibility that, during periods of snowcover, lynx may occur more often in areas in which they have a competitive advantage over coyotes. Snow Water Equivalent measurements of 5.08 cm (2 inches) were recommended for use as a provisional threshold for representing motive advantage of lynx over coyotes (P. Farnes, Hydrologist, Snowcap Hydrology, 15 October 2003, conversation).

Consequently, working definitions for winter and summer were distinguished by the two dates (18 November and 9 May) between which daily SWE measurements at the sole SNOTEL station in the study area exceeded 5.08 cm when averaged over the years of the telemetry studies.[16] By these dates, 291 points were designated as winter locations and 542 points as summer locations. 50% of the points from each seasonal subset were then randomly selected, then removed and combined for use as an independent evaluation dataset.

Resource Selection Analyses

Several comparative studies of common statistical techniques for analysis of habitat selection have demonstrated that different methods can yield conflicting results (Alldredge and Ratti 1986, 1992; Manly et al. 1993; McClean et al. 1997). For this reason, several methods were used in this study, including compositional analysis (Aebischer et al. 1993), χ^2 tests of independence, and the Neu et al. (1974) method (Neu's method). This facilitated comparison of lynx selection patterns as based on the three methods and helped to corroborate final selection of predictor datasets as Bayes inputs.

Considerations that should guide the choice of analysis methods include the hypotheses being tested and the validity of the requisite assumptions (Alldredge et al. 1998). With respect to hypotheses, the three methods used in this study are those which most explicitly test selection according to the definition given by Johnson (1980), namely that habitat types are used disproportionately to their availability (Alldredge et al. 1998).

Key assumptions of the two methods based on χ^2 distributions (i.e., χ^2 tests of independence and Neu's method) include: (1) minimum expected frequencies, (2) >= 50 relocations for each of >= 20 individuals (Alldredge et al. 1998), (3) spatial and temporal independence of observations, (4) habitat availability which is known, constant, and common for all individuals (Alldredge et al. 1998), and (5) independent selection of habitat by different individuals (violated when animals are gregarious or territorial). Of these, compositional analysis relies only upon assumption (5).

Requirements (1) and (2) were satisfied in that all frequencies of lynx presence were measured as areas rather than counts. On logistical grounds, it is likely that assumption (3) is violated by all studies involving radio-collared individuals; in this case however, the vagility of lynx combined with the low frequency of relocations (see Appendix A) led to the conclusion that any spatial and serial correlation between observations was negligibly low. Assumption (4), which in this study pertains only to meso-scale selection, was met through use of a constant definition for the meso-scale zone of availability. Assumption (5) was considered satisfied on account that the locational effects of any behavioral spacing mechanisms with resident lynx are likely to be overwhelmed by local environmental factors such as snowshoe hare densities (Ward and Krebs 1985).

Compositional analysis is a multivariate method that tests whether the utilized log-ratio data matrices (compositions) differ from the available habitat log-ratio data matrices. Unlike Neu's method, compositional analysis directly addresses the unit-sum constraint (Aebischer et al. 1993), by which the proportions that detail habitat composition sum to one over all classes in a predictor dataset. Thus, disproportionate use versus availability of any habitat type is determined in accord with consideration of the utilization of other habitat types. The logarithmic transformation in compositional analysis requires that each individual use all habitat types. Therefore, a small value (0.0001) was substituted for instances where proportional habitat use was estimated as zero (after Aebischer et al. 1993).

Application of the χ^2 tests followed Aspinall (1992a) – after conditional probabilities (or, frequencies of association) are assigned to each class in a predictor dataset, χ^2 analysis is used to test the significance of the predictor dataset for discriminating between lynx presence and randomness. Neu's method also involves application of the χ^2 test; however, when a significant difference is detected between habitat utilization and availability for a predictor dataset, a Bonferroni Z-statistic is applied to generate confidence limits by which to determine specific classes that are occupied more or less frequently than expected.

Testing by each method was conducted against the 15 predictor datasets in accord with all 32 defined instances of lynx presence and habitat availability.[17] Compositional analyses and χ^2 tests were conducted at $\alpha = 0.1$, while Neu's method was applied using a 90% Bonferroni confidence interval.

As noted previously, each predictor variable was represented by a series of either two or three alternative datasets. Testing was performed across each series and the dataset with the narrowest class intervals that yielded one or more significant associations was identified for review as a potential Bayes model input. This iterative procedure assured the optimal use of available information content in the original predictor data.

Bayesian Modeling

Rule-based Determination of Bayes Model Inputs

Designation of inputs for each Bayes model was based on a rule-based review of results from the three selection analysis methods (see Appendix D). A predictor dataset was assigned as an input layer only if compositional analysis and at least one of the two χ^2 -based methods (χ^2, and Neu's) had detected it to have (or contain) a significant association with lynx presence. To mitigate for potential "noise" or artifacts in the data, significantly discriminatory classes identified by compositional analysis or Neu's method were considered only if they composed >= 1% of all available classes in a predictor dataset.

By this protocol, 32 combinations of predictor datasets were identified, each corresponding with a defined instance of lynx presence and habitat availability across the three selection scenarios: 20 cases for the first selection scenario (i.e., selection by ten individuals at both scales), 10 cases for the second scenario (i.e., selection by five individuals at both scales), and 2 cases for the third scenario (i.e., seasonal selection at one spatial scale using pooled data from the 22 lynx).

Generation, Aggregation and Evaluation of Bayes models

Using these combinations of predictor datasets, 32 corresponding Bayes models were generated using the Bayes Extension for ArcView (Aspinall 2000) and grouped by selection scenario (see Appendix E). Models from each scenario were then combined into three respective aggregate models. Cell values in these aggregate models were calculated as the *focal maximum* taken across each corresponding set of input models.

Testing of the aggregate models was conducted using independent datasets of known lynx presence. Lynx presence in the first and second test datasets (Figures 5a and 5b) were defined, respectively, by the areas formed by 200 m buffers around radiolocations from the 12 least-sampled lynx (n = 307) and those from the 17 least-sampled lynx (n = 525).18 This basis wholly on individuals excluded from the generation of models was necessitated by the relatively low representation of individual lynx. The third test dataset (Figure 5c) was based on 50% of the radiolocations from each season as initially removed from the original dataset (n = 145 for winter,

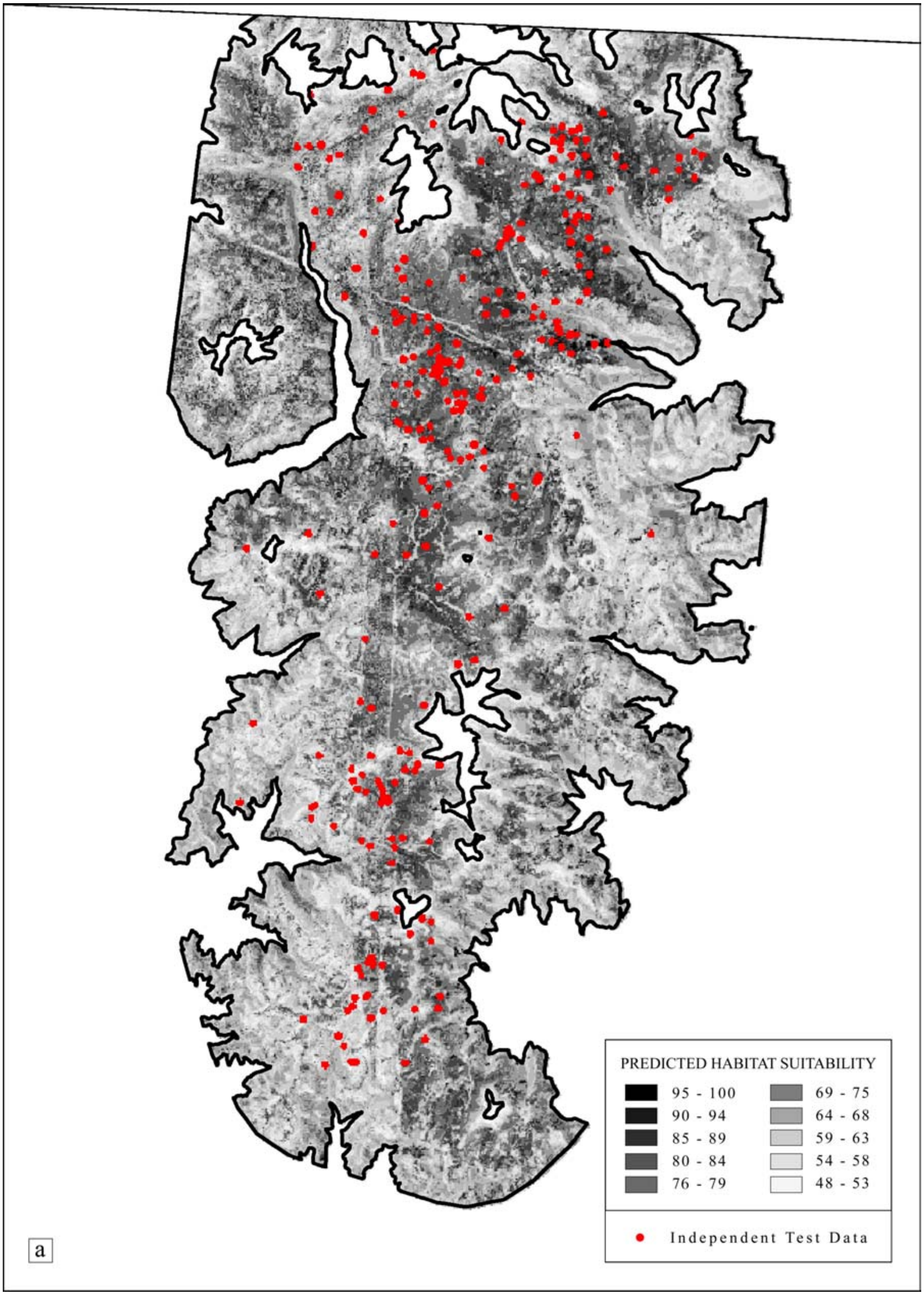


Figure 5a – Selection Scenario One: Aggregate Bayes model and test dataset

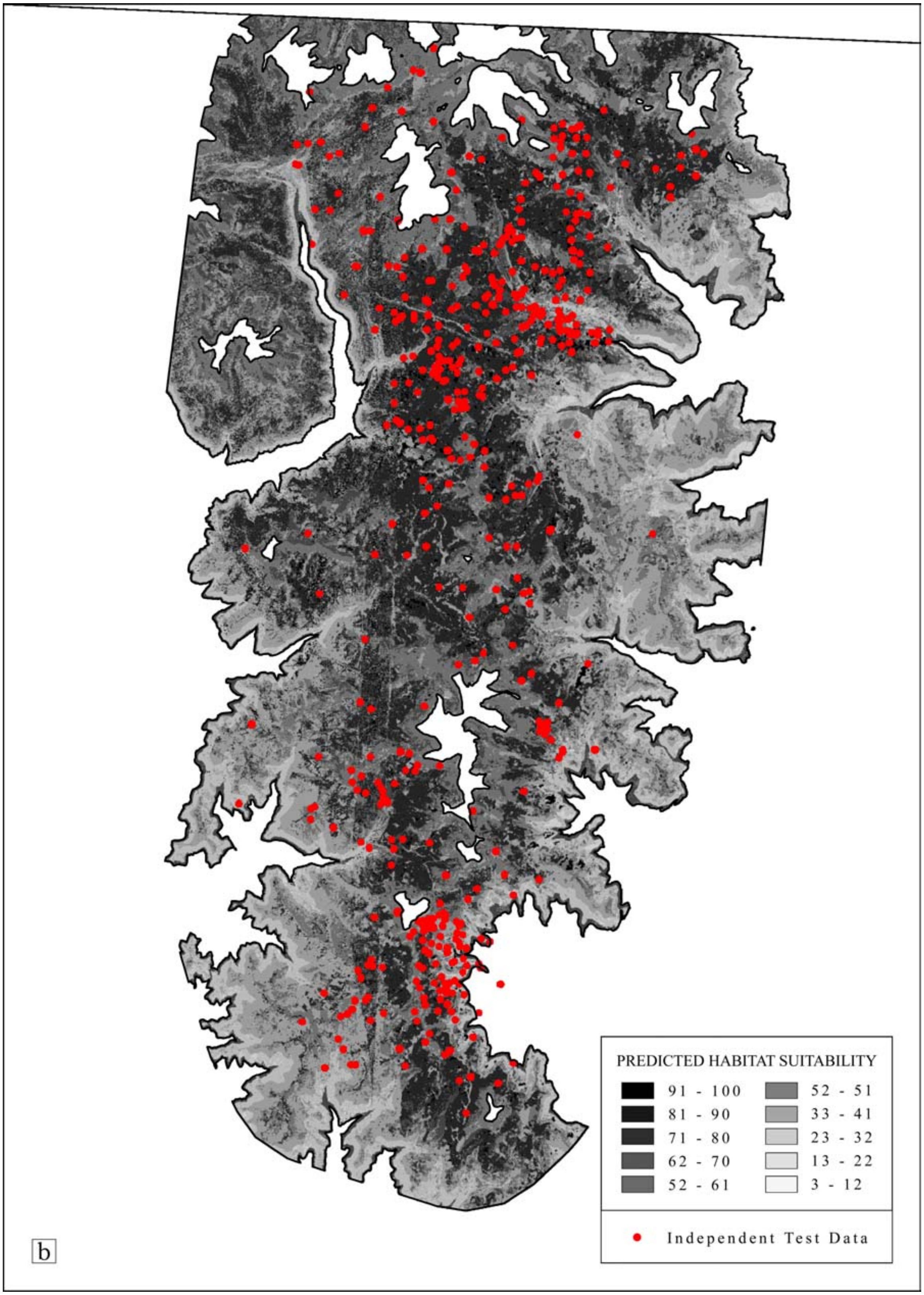


Figure 5b – Selection Scenario Two: Aggregate Bayes model and test dataset

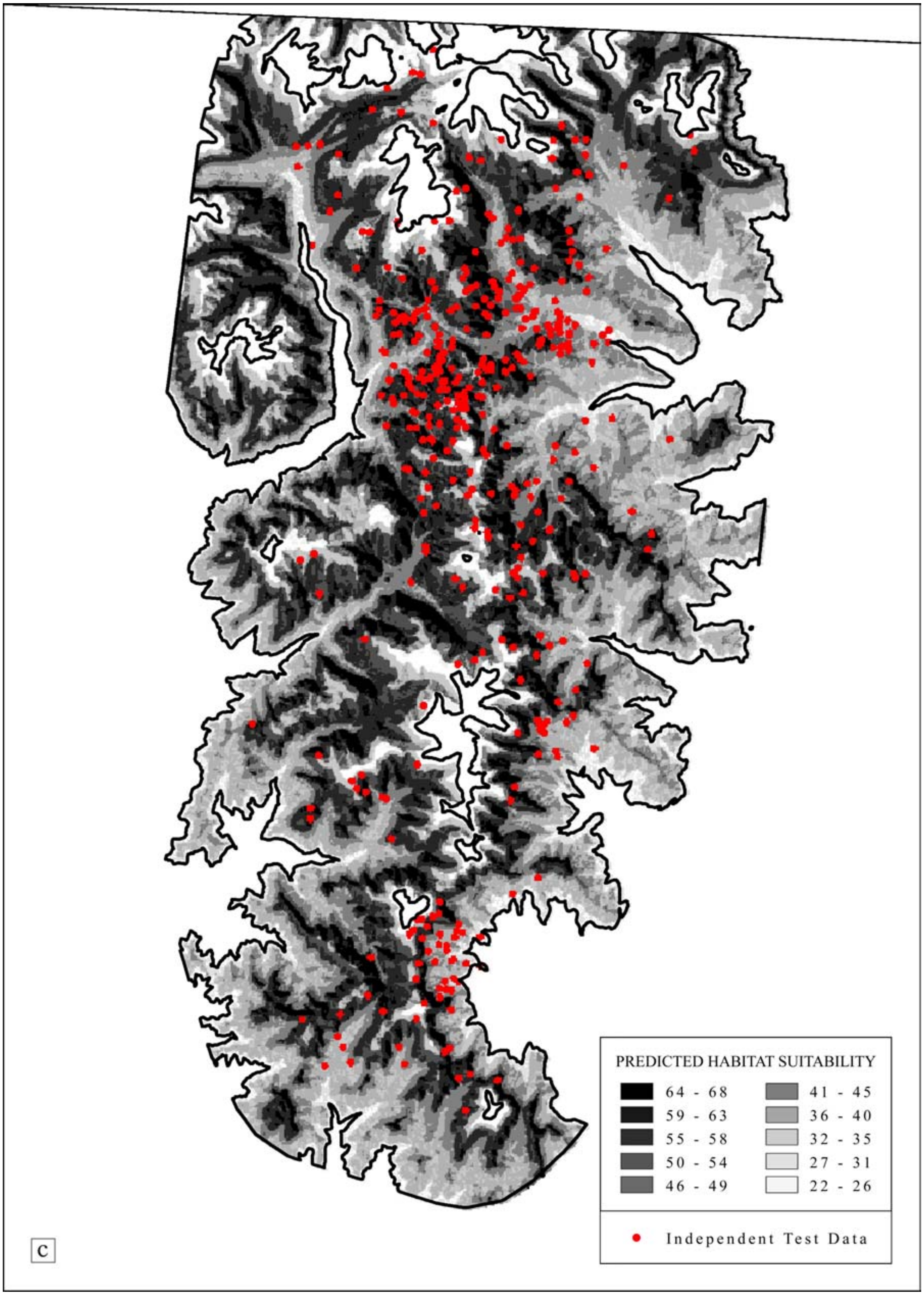


Figure 5c – Selection Scenario Three: Aggregate Bayes model and test dataset *n* = 270 for summer); lynx presence was defined by the areas formed by 200 m buffers around these combined locations (*n* = 415).

Evaluation indicated that the first aggregate model was more predictive of lynx presence in its respective test dataset than were the second and third aggregate models (see Results); therefore, this first model (i.e., that from Selection Scenario One) provided the basis for all subsequent analyses in this study.

To further characterize this final model, two additional grids were generated to assess cell-by-cell variation across its 20 constituent Bayes models. Cell values for the first were assigned as the *focal mean* calculated across the separate models (Figure 6a), while values for the second were assigned by their *focal standard deviation* (Figure 6b). Taken together, these two grids express the uncertainty in habitat suitability as modeled between lynx for any given location in the final model. Higher values in the focal mean grid are found nearer the core of the study area; this reflects the general spatial distribution of values in the aggregate model and confirms that higher suitability values are corroborated with greater “concurrence” between lynx. In marked contrast, higher values in the focal standard deviation grid occur along the periphery of the study area, indicating that variability is greater where predicted suitability is relatively low. The greater accord in lynx preference in areas of higher suitability lends support to the use of those areas for the definition of habitat patches.

Preparation of an Impedance Surface and Habitat Patches

The two elements needed to form the framework for the connectivity analyses, an interpatch cost surface and the habitat patches themselves, were both derived from the final aggregate habitat suitability model. To generate the cost surface, the range of suitability values (0 – 100) in

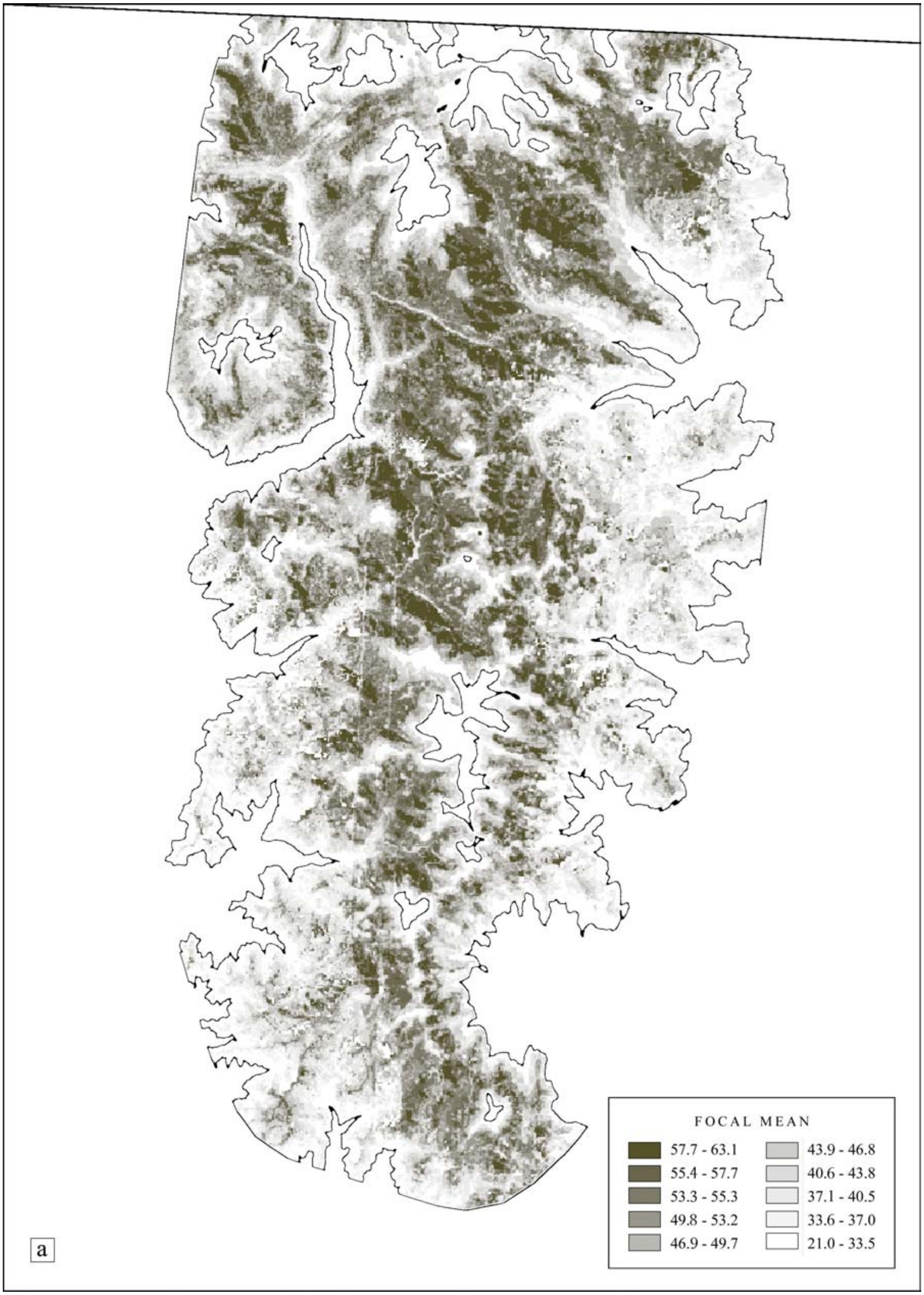


Figure 6a – Focal mean surface associated with the selected aggregate Bayes model

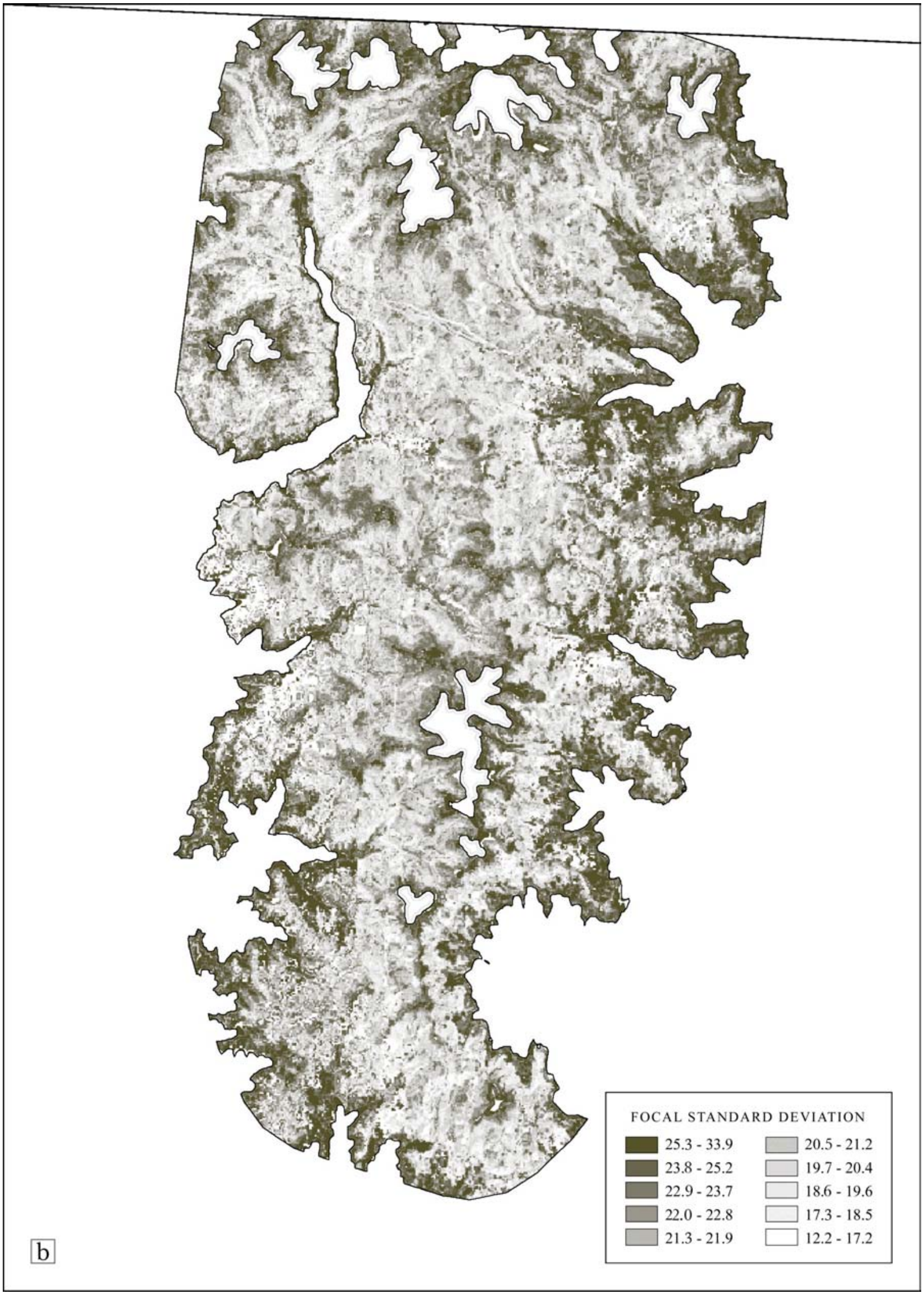


Figure 6b – Focal standard deviation surface associated with the selected aggregate Bayes model the aggregate model was inverted to comprise values (100 – 0) representing high to low costs to movement, or impedance (Figure 7).

Extension of the Impedance Surface

Initially, impedance values existed only to the limits of the meso-scale zone of availability. In order to allow for interpatch linkages occurring across areas outside this zone (including across elevations < 1350 m and > 2150 m), it was necessary to extend the impedance surface through supplemental selection analyses conducted within a broadened zone of availability.[19] Expansion of the zone was made at the mean minimum daily distance (MDD) of the five lynx with >= 49 locations — the implicit assumption in this being that functional interpatch linkages would not exceed the Euclidean distance a resident individual might be expected to traverse in a 24-hour period. Combining the distances between all pairs of consecutive daily radiolocations from the five lynx yielded a mean distance of 2.38 km (*n* = 31, SD = 1.36, range = 4.99 km); this compares to a mean MDD of 2.25 km for the ten lynx with >= 39 locations (*n* = 53, SD = 1.63, range = 8.3 km), a mean MDD of 2.40 km for all lynx in this study (*n* = 76, SD = 1.89, range = 8.69 km), and a mean MDD of 3.4 km (*n* = 941) documented by Apps (2000) for radio-collared lynx in the southern Canadian Rockies.

Supplemental analyses were conducted for Johnson's second-order selection within the expanded meso-scale zone of availability, where lynx presence was defined by the fixed kernal home range estimates for each of the five individuals (Figure 8a). Determination of predictor datasets as inputs for each Bayes model followed the same rule-based review as had the prior selection analyses. Once the new Bayes models were generated, aggregated according to their focal maximum, and inverted to impedance values, the resulting surface was masked to exclude the original meso-scale zone of availability (Figure 8b).

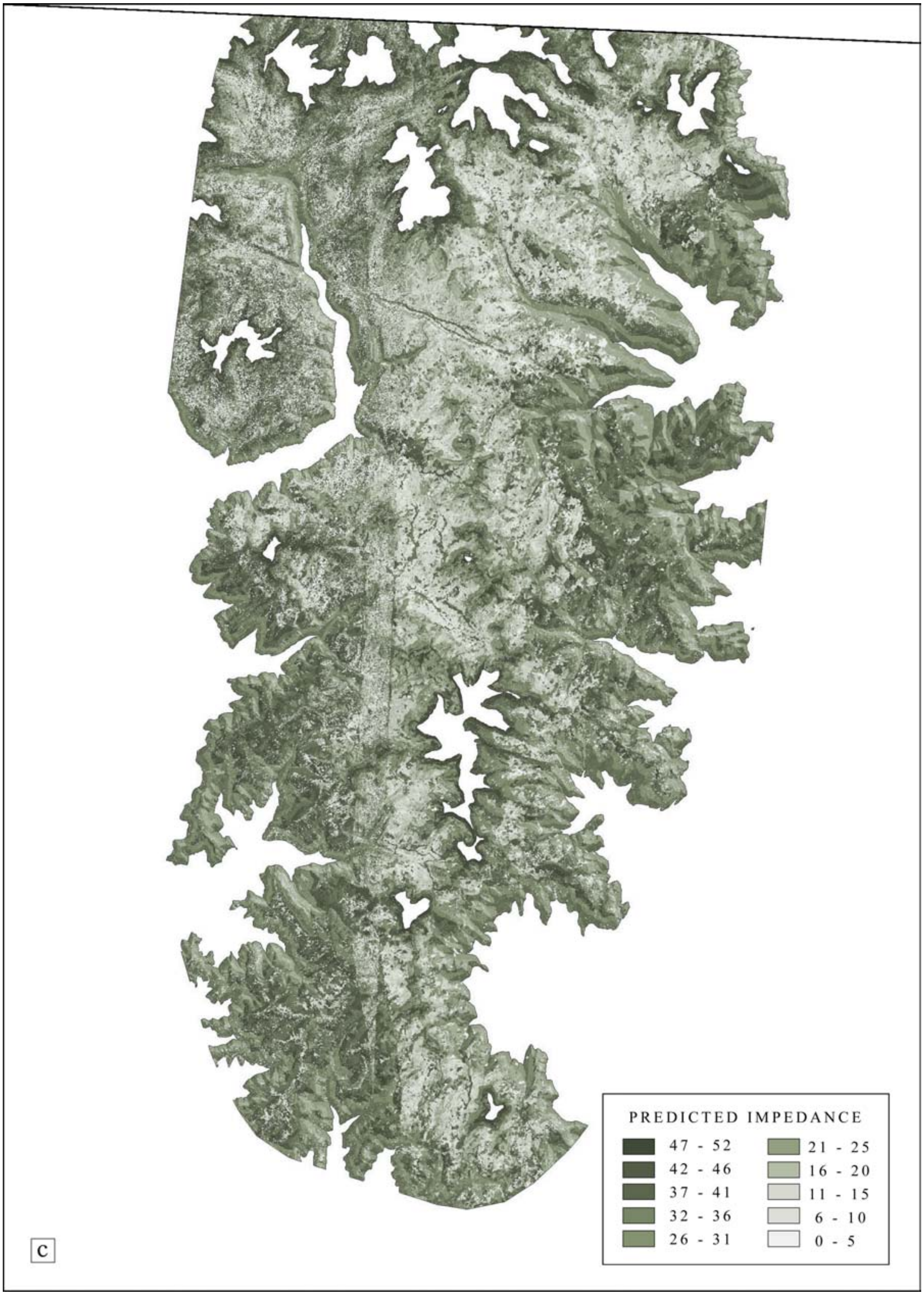


Figure 7 – Original impedance surface

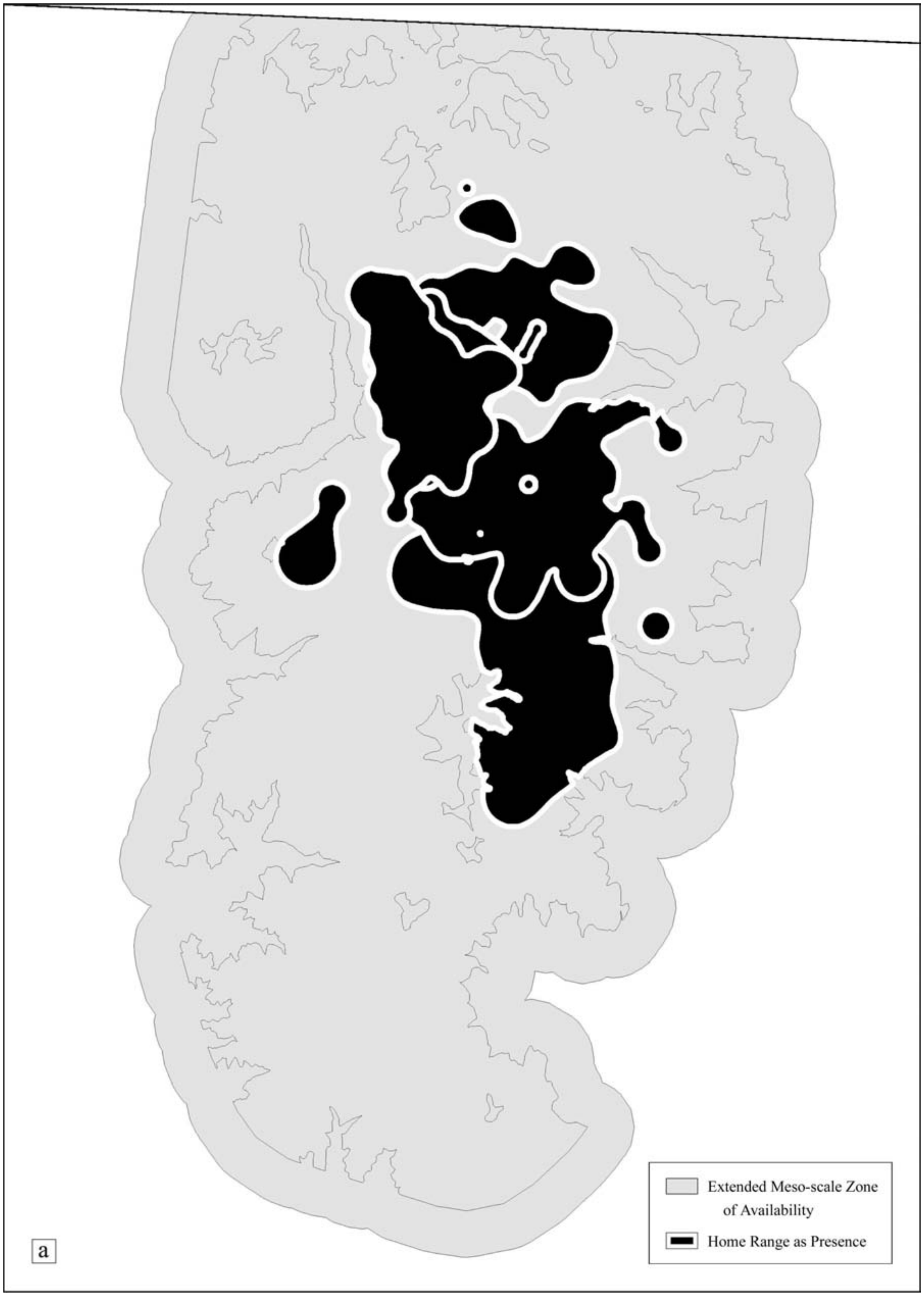


Figure 8a – Selection scenario for expansion of the original impedance surface

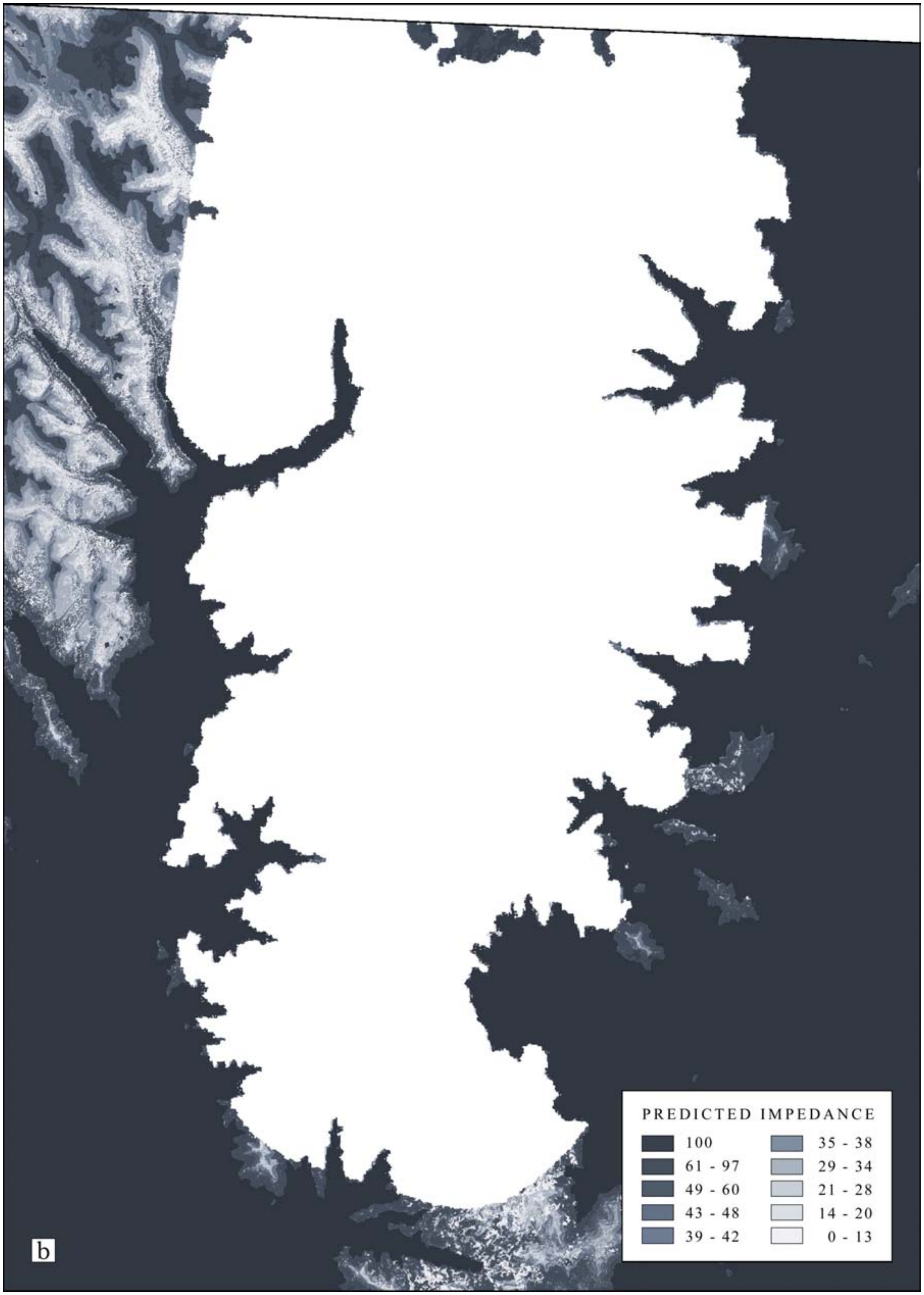


Figure 8b – First impedance surface for outlying areas

Due to the effects of exceedingly low conditional probabilities calculated for lynx and elevation classes < 1350 m and > 2150 m, impedance in these areas was nearly uniform and prohibitively high. In order to assign cost values to these areas that could allow for possible exploratory movements by lynx, a second surface for outlying areas was required. Its generation followed that of the first extended surface, with the exception that elevation was excluded from the Bayes modeling. After the resulting cost surface was generated, it was masked to exclude both the original meso-scale zone of availability and all areas with elevations between 1350 m and 2150 m, then combined with the first extended surface (Figure 8c). Finally, this composite surface for outlying areas was combined with the initial impedance surface to compose the final impedance surface (Figure 8d).

Patch Delineation

To generate habitat patches directly from a Bayes model, its range of values must be converted to a binary classification (i.e., denoting patches versus the intervening gaps or matrix) using a selected threshold suitability (or, probability) value. In order to better address intra-patch variation as well as uncertainty in the distinction of actual habitat patches, patch boundaries, and landcover classification, this study used a range of ten alternate patch surfaces (Figure 9).

In deriving each of these patch surfaces, a suitability threshold was applied to each of the 20 individual Bayes models. The threshold for each was specified as the highest (and thus most restrictive) suitability value which still encompassed a set minimum percentage of the area occupied by lynx according to the model's instance of known lynx presence (see Appendix F). (Hereafter, these minimum percentages are referred to as "area-of-presence thresholds"). Each of the ten pairs of initial binary surfaces were then combined per their *focal sum*, such that patches in the resulting ten combined surfaces existed only where defined by the area-of-presence threshold

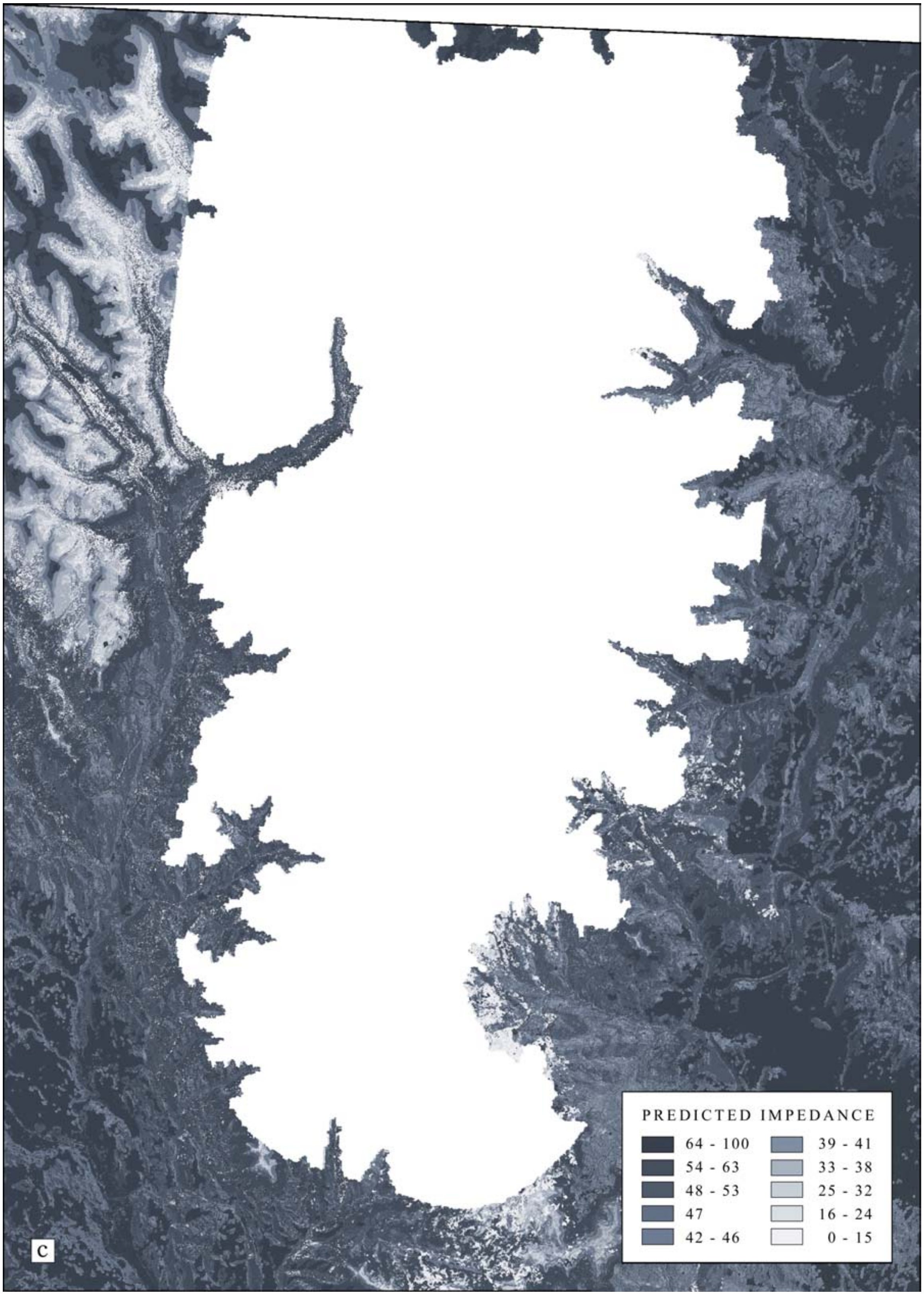


Figure 8c – Second (and composite) impedance surface for outlying areas

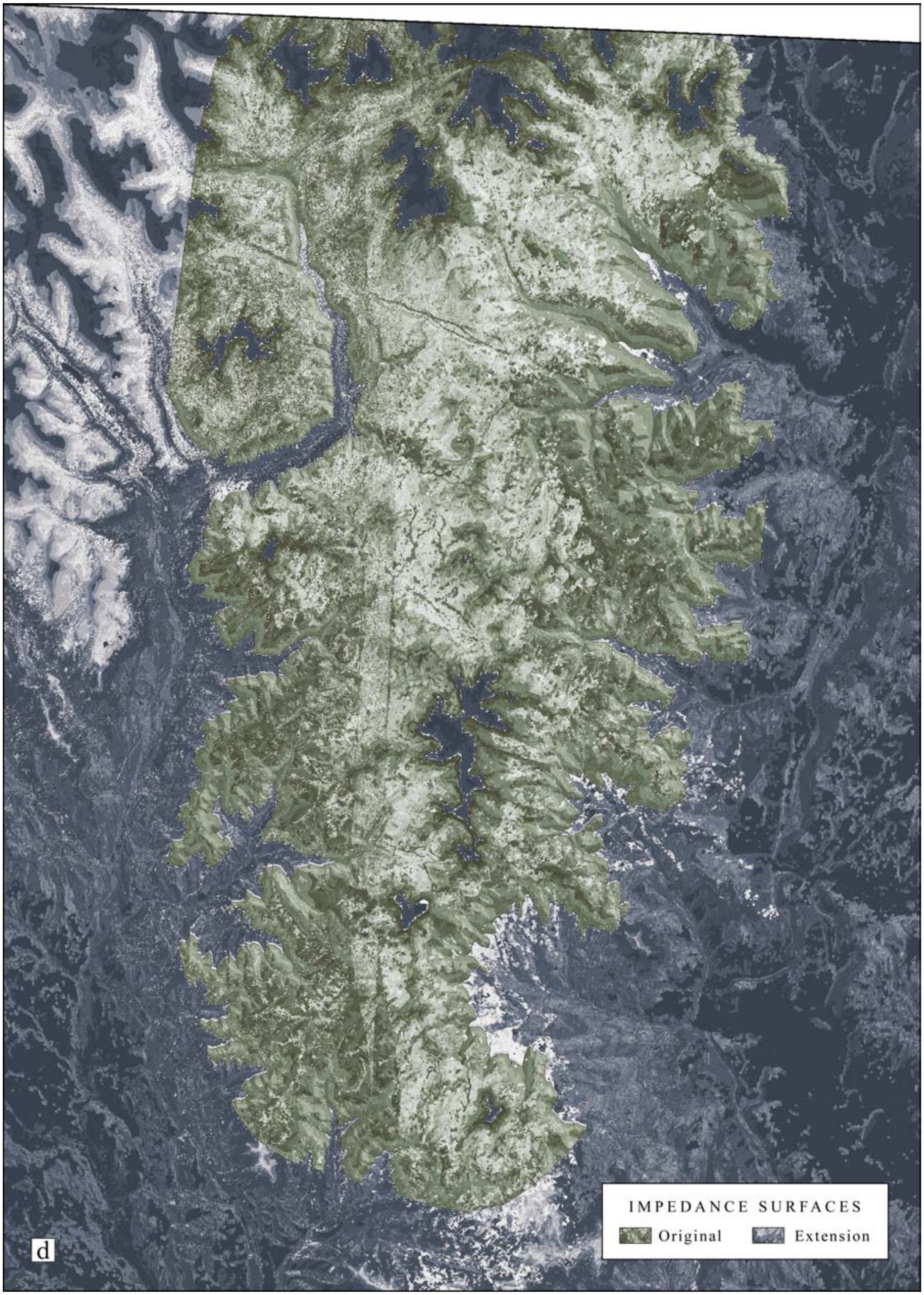


Figure 8d – Second impedance surface for outlying areas and the original impedance surface

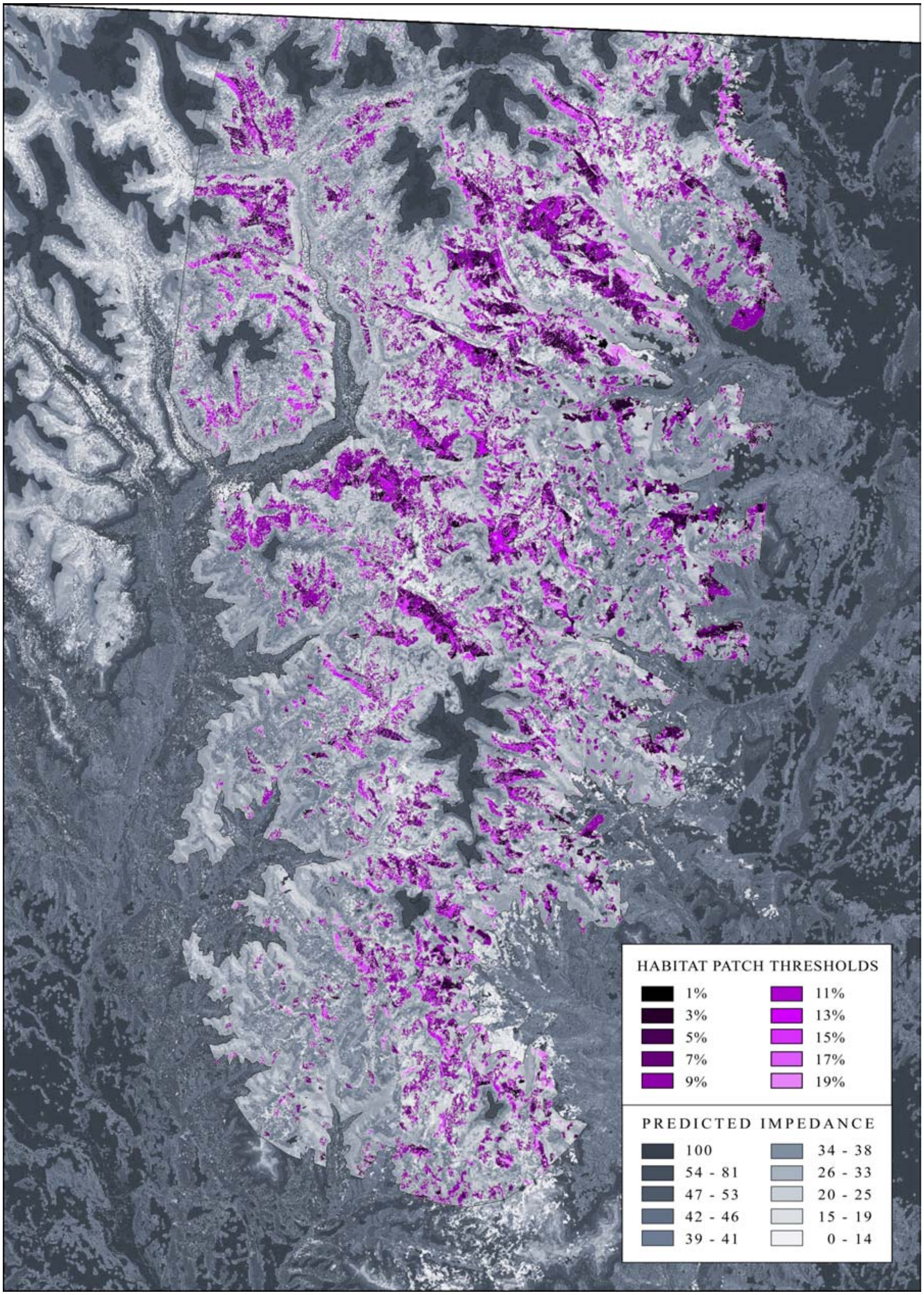


Figure 9 – Study-wide patch surfaces (shown pyramidally) over the final impedance surface

for a given lynx at both scales of selection. These individual-based patch surfaces were then combined per their focal maximum into a final patch surface.

In all, ten area-of-presence thresholds were used (1%, 3%, 5%, ... , 19%), resulting in ten corresponding final patch surfaces at the extent of the meso-scale zone of availability. To each of these surfaces a minimum patch size was then applied. Because a review of the literature did not reveal any estimates of a minimum patch size requirement for lynx, 2.78 ha was chosen as an acceptable approximation, being the area in which (human) capture of snowshoe hare was computed at 0.8 probability in a study in Alaska by Wolff (1980).[20]

In preparation for analysis of connectivity within each of the ten estimated home ranges, ten additional patch surfaces were generated from the individual-based Bayes models based on fine-scale selection. A 7% area-of-presence threshold was used for all fine-scale patch delineations because its respective study-wide patch surface contained the associated extent of known lynx presence within a disproportionately low total area (Figures 10 and 11).

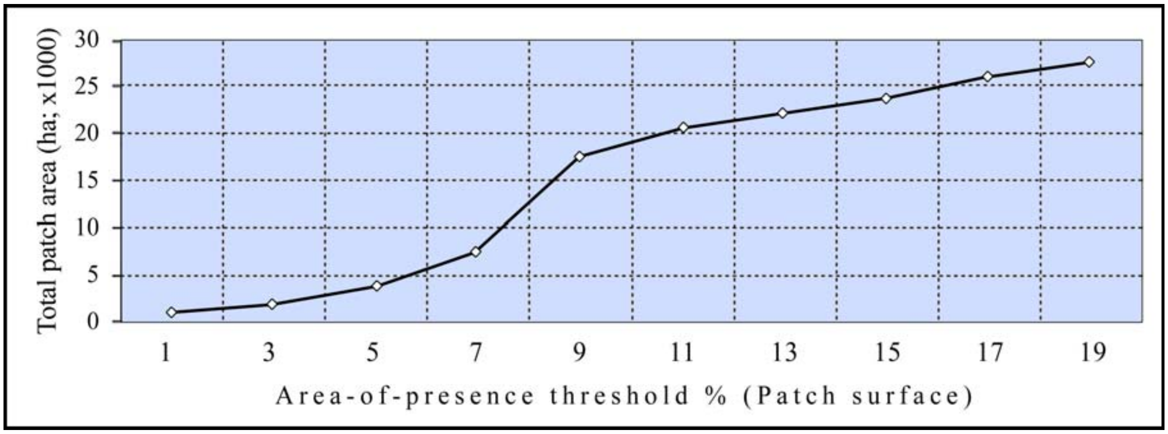


Figure 10 – Total areas of study-wide patch surfaces

Figure 11 – Within-home-range patch surfaces

Graph-Theoretic Modeling

Graph Generation

Beginning this study's second phase, the final impedance surface was paired with each of the 20 final (multi-scale and fine-scale) patch surfaces. Twenty corresponding "pre-graph" networks were then generated using an Avenue script (R. J. Aspinall, author) (Figure 12a). Nodes in these networks were formulated as patch centroids, while inter-node links represented all possible connections between nodes of proximate patches as determined by the Thiessen polygon method. Pre-graph networks provided the groundwork for derivation of graphs in accord with varying

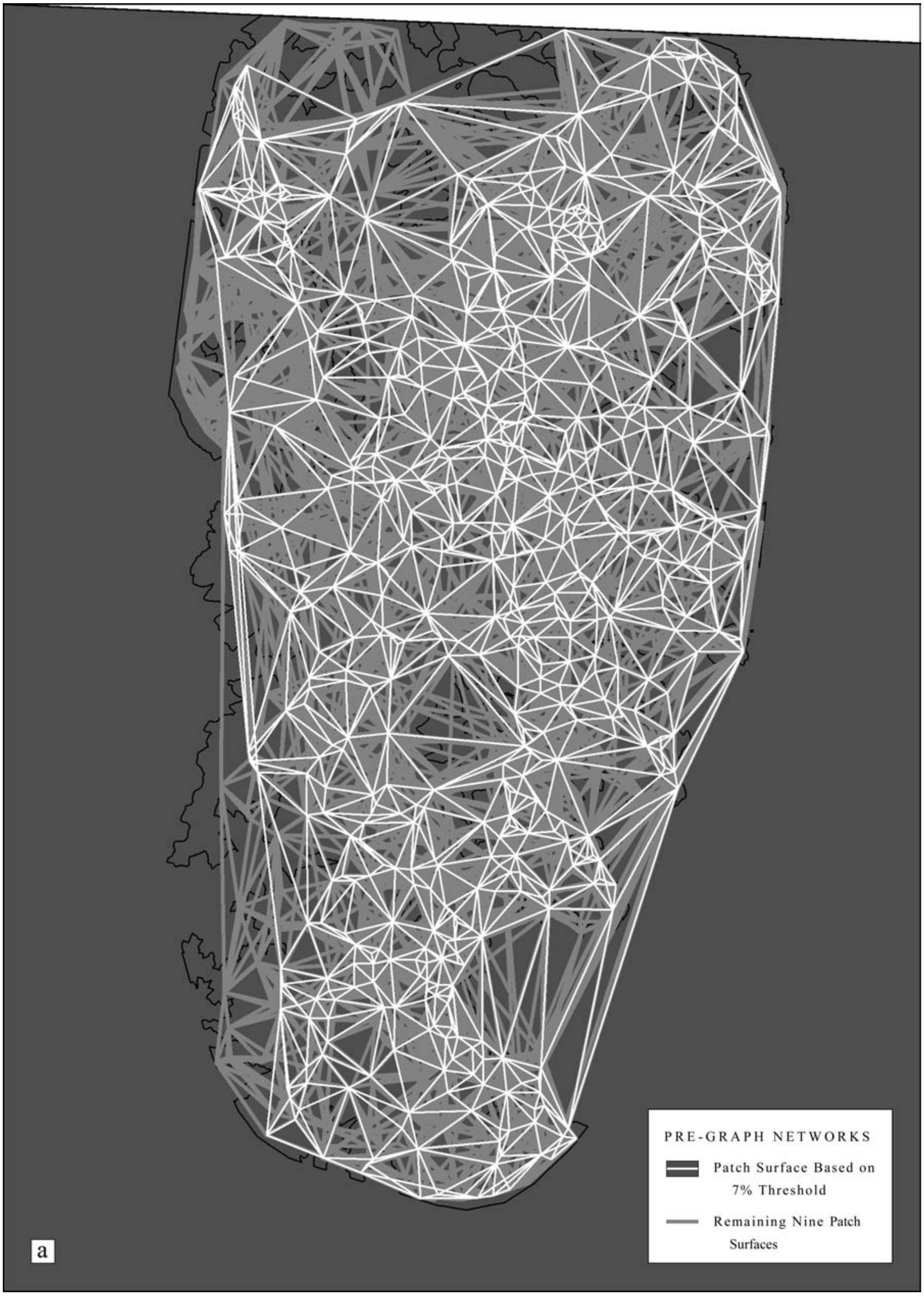


Figure 12a – Study-wide pre-graph networks definitions for node adjacencies. As noted previously, graphs in this study were formed from adjacencies determined in accord with one of two alternate definitions for functional interpatch distances: d_{ij} measured as least-cost (patch)edge-to-(patch)edge distances, and p_{ij}, or dispersal probabilities, measured as d_{ij} modified by a coefficient for negative-exponential decay.

Study-wide Connectivity by Patch Definition

The documented mean MDD from all sampled individuals (here, 2.40 km) provides a benchmark interpatch distance for evaluating study-wide, multi-scalar habitat connectivity (Figure 12b).[21] Using this as a threshold edge distance d_{ij}, one graph was generated for each of the ten study-wide pre-graph networks. The effective connectivity of each graph was then summarized with three metrics – the number of its components, its traversability (i.e., the longest diameter from among its components), and its average connectivity (see Results). Derivation of the latter two metrics was accomplished using the Combinatorica extension for Mathematica (Wolfram 2001; also see Skiena 1990).

Identification of Core Linkages

The minimum spanning tree (or, MST) of a graph is a relatively straightforward construct that can be taken to represent its "parsimoniously-connected backbone" (Bunn et al. 2000; Urban and Keitt 2001). Using a Visual Basic executable (R. J. Aspinall, author), two sets of MSTs were identified for the ten study-wide pre-graph networks;[22] MSTs in the first set were generated using distances d_{ij} and those in the second set were predicated on dispersal probabilities, p_{ij}, where the distance-decay coefficient, ϕ, was set to the mean MDD of 2.40 km (Figure 13a). All MSTs based on distances p_{ij} were subject to a considerable boundary effect; consequently, all subsequent attention was given to those based on distances d_{ij}.

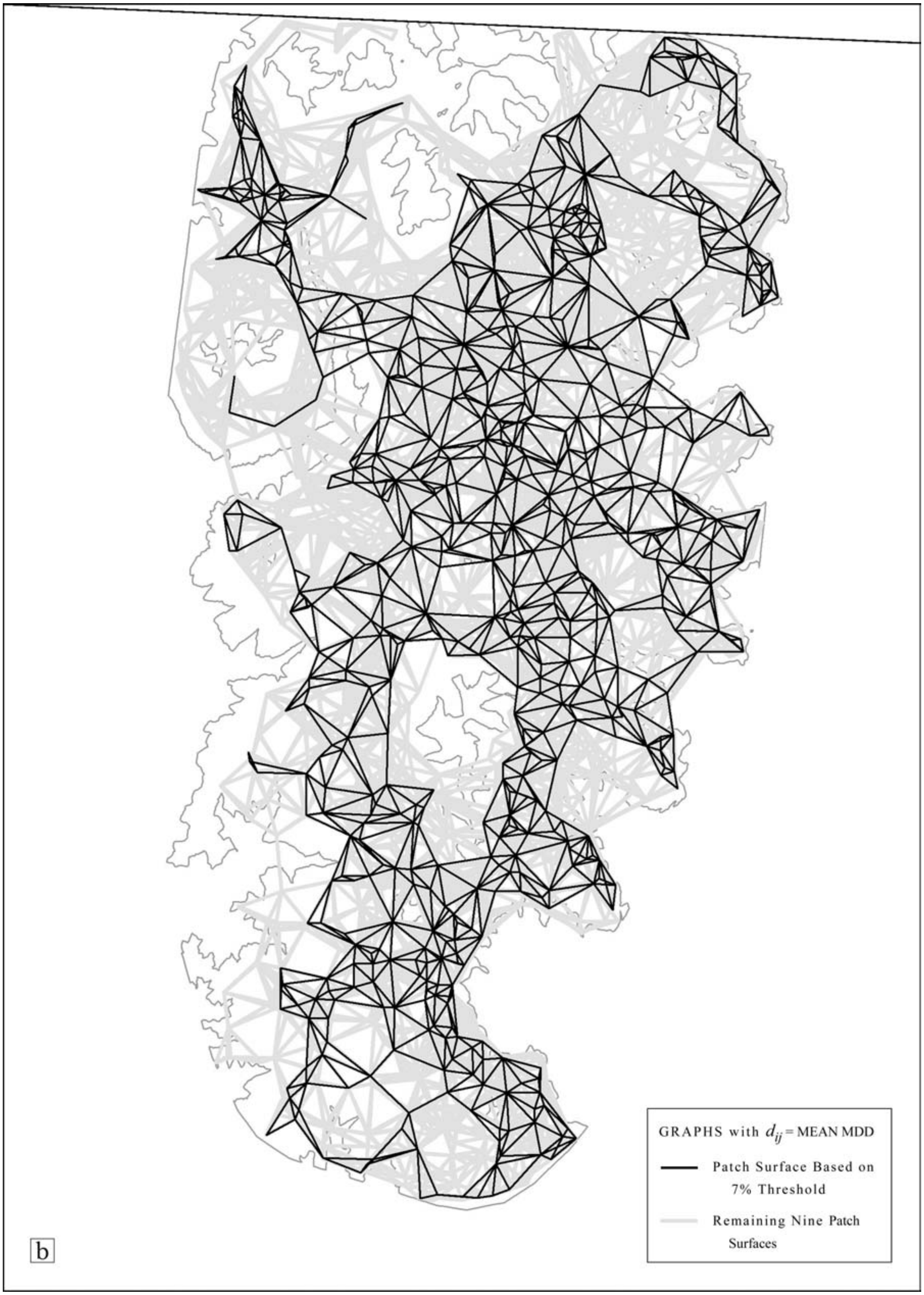


Figure 12b – Study-wide graphs with interpatch distances set to the mean MDD

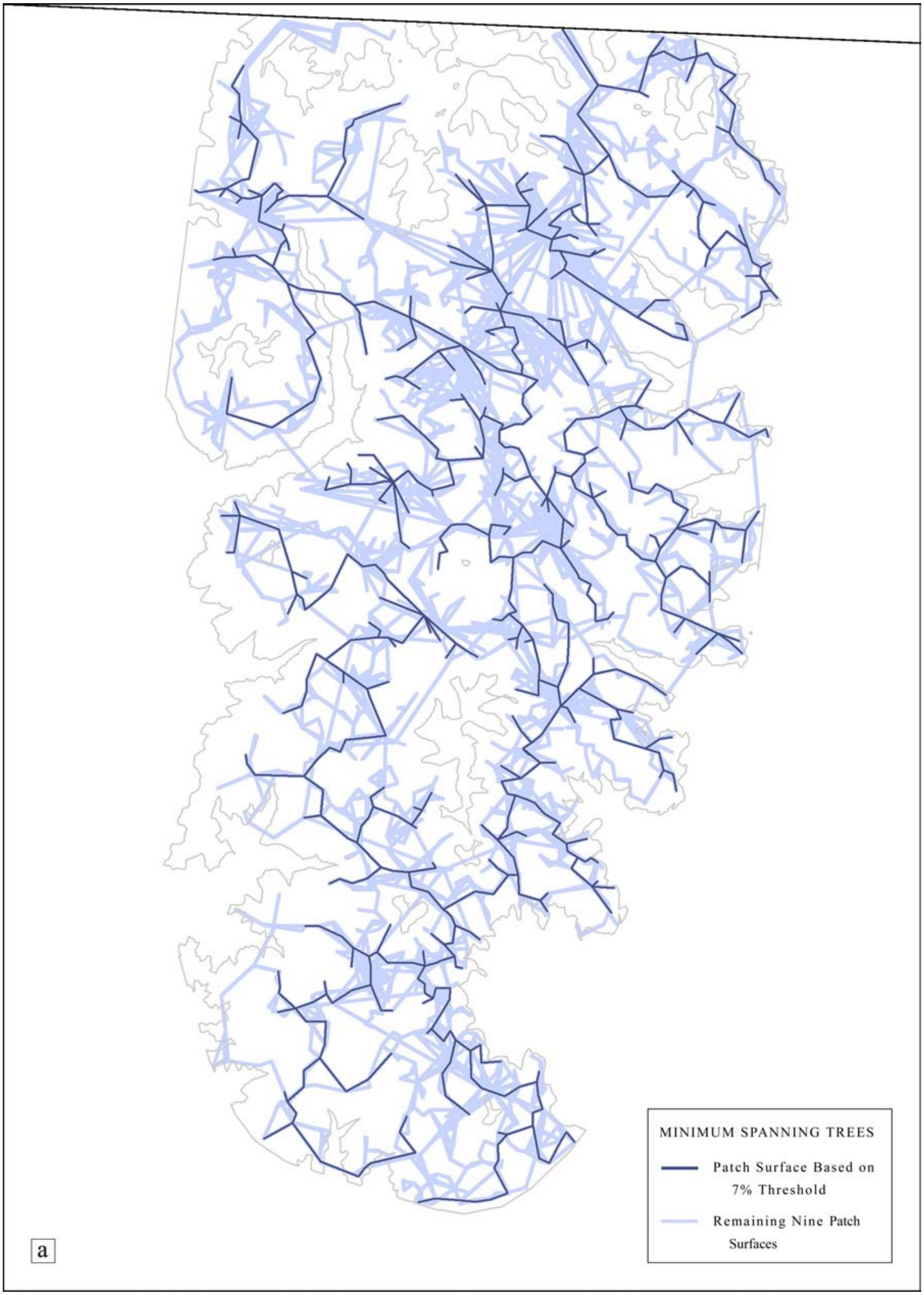


Figure 13a – Study-wide minimum spanning trees

To represent core connectivity within individual home ranges, MSTs were found for each of the ten fine-scale pre-graph networks using distances d_{ij} (Figure 13b).

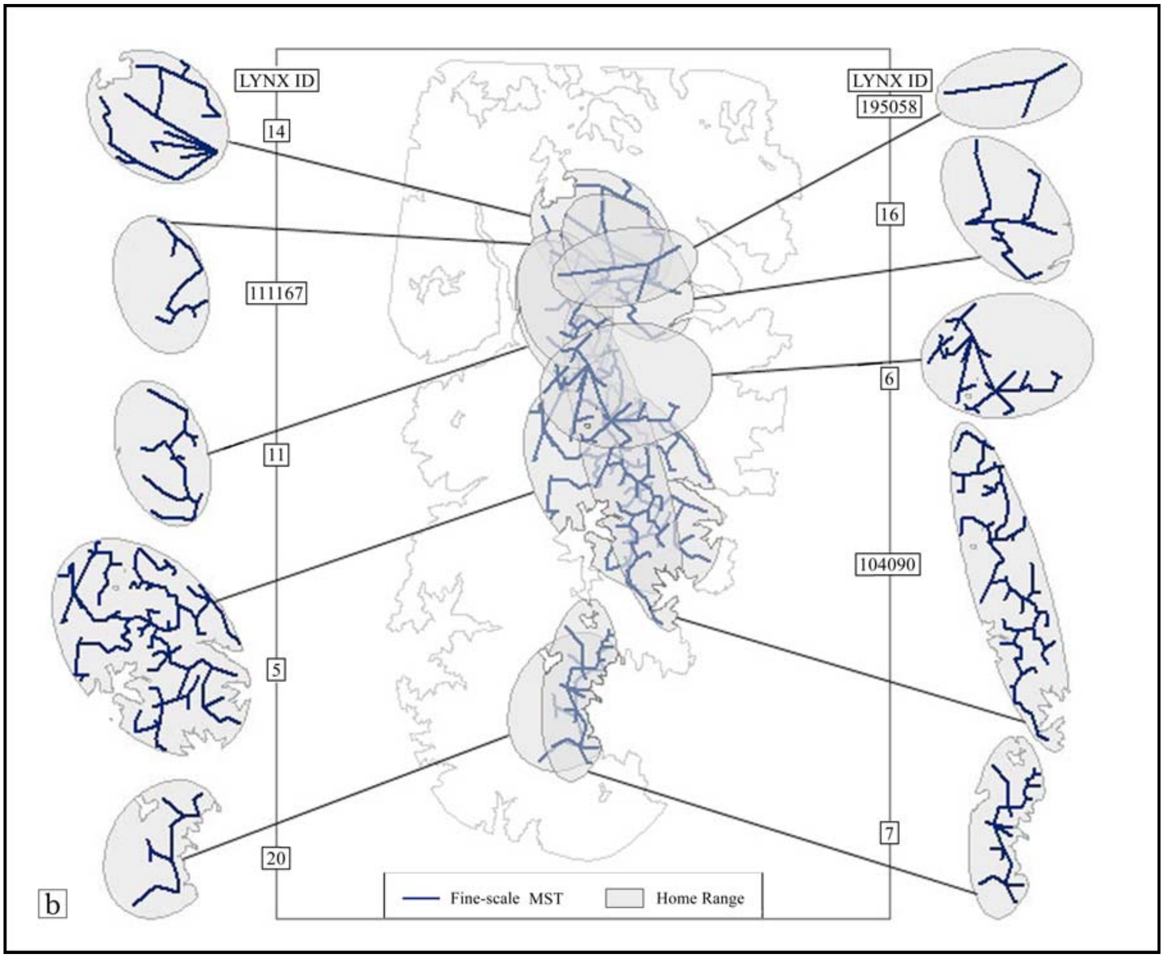


Figure 13b – Within-home-range minimum spanning trees

Prediction of Weakest Linkages

To identify cut-edges representing linkages most susceptible to disruption, edge-thresholding was conducted on the five study-wide graphs generated from functional interpatch distances d_{ij} and originating from the five most restrictive patch surfaces (i.e, those defined at area-of presence thresholds 1%, 3%, 5%, 7%, and 9%)(Figure 14). Initial edge distances were set such that each graph was fully connected. Edges were then iteratively removed with edge

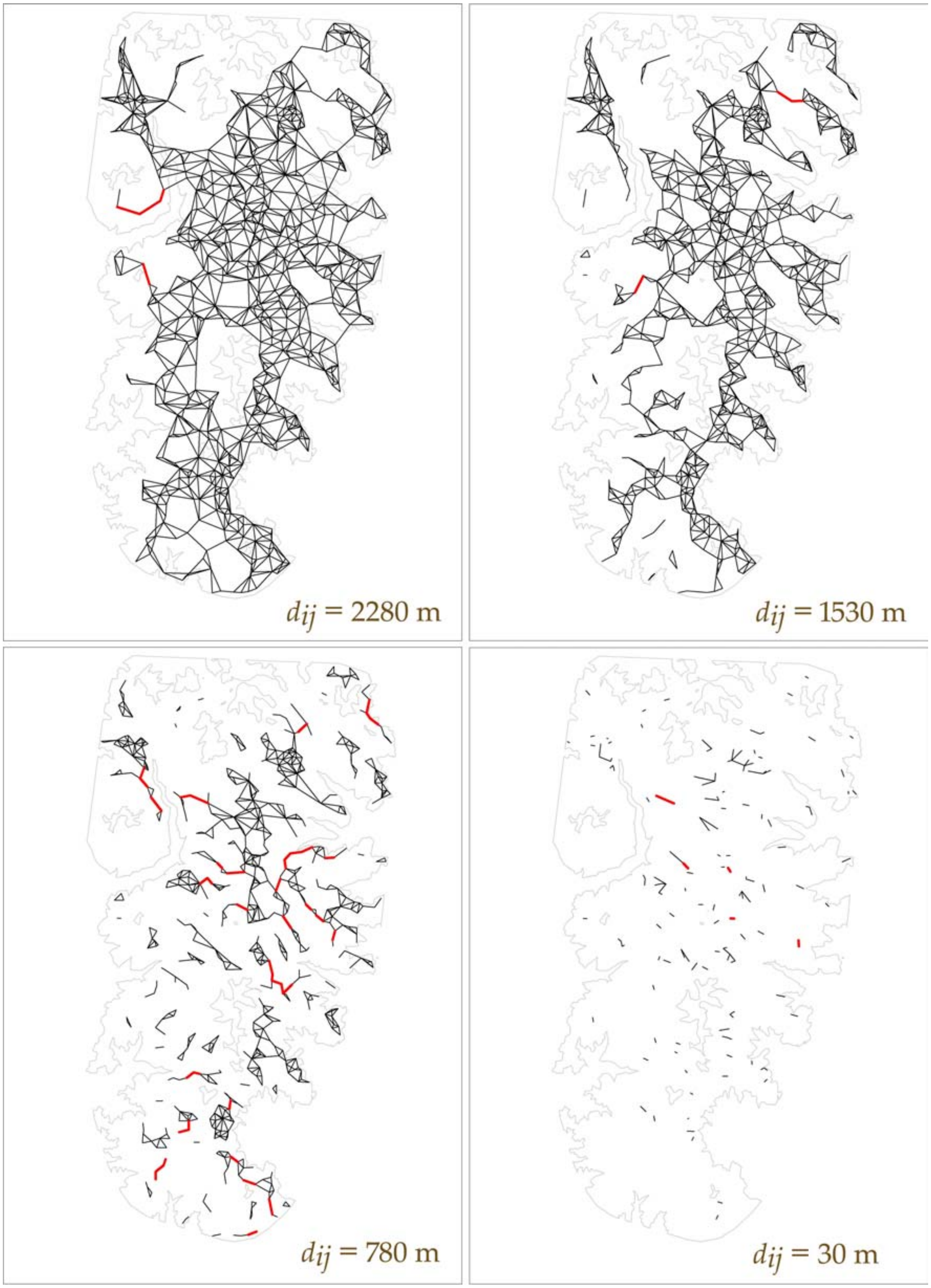


Figure 14 – Edge-thresholding for the study-wide graph derived from the 7% area-of-presence threshold (see Appendix G for full iteration set)

distance thresholds lowered at 50 m intervals. With each iteration, every cut-bridge incident to (two) components of a set minimum diameter of 760 m was identified. Use of a minimum diameter here was necessary to highlight more important cut-edges (i.e., those connecting larger patch networks) while preventing the noise posed by those connecting already diffuse fragments of patch networks. Specification at 760 m was discretional, this being approximately one quarter the threshold distance of each of the five graphs when fully *connected.* Iterations continued on each graph until the critical interpatch distance reached 30 m, the interval nearest to zero (Figure 15a).

Important fine-scale linkages were then predicted by edge-thresholding graphs from the ten individual-based, within-home-range networks (Figure 15b). As with the study-wide graphs, edge distance thresholds were initially set so that each graph was fully connected, then iteratively reduced by 50 m intervals until the lowest threshold distance of 30 m was reached. Again at each step, all cut-bridges incident to components with a minimum 760 m diameter were recorded.

Mapping of Study-wide Edge Densities

Comparison among MSTs and cut-edges derived from alternate patch surfaces can provide a limited means of assessing the sensitivity of these graph constructs to patch definitions. However, given the uncertainty inherent to any definition for actual habitat patches, it is desirable to interpret the spatial co-occurrence of these constructs simultaneously as they arise across all ten patch surfaces. Simple overlays of the graph constructs, however, were not given to effective pattern recognition by reason of the number of patch surfaces and the intrinsic displacement of corresponding nodes (and edges) between each respective network.[23] Therefore, to enable more practical and integrated interpretation, line density surfaces were generated (search radius = 2500 m) for each set of constructs. In these, only “high” densities (defined as >= 1.5 SD) were considered for interpretive purposes.

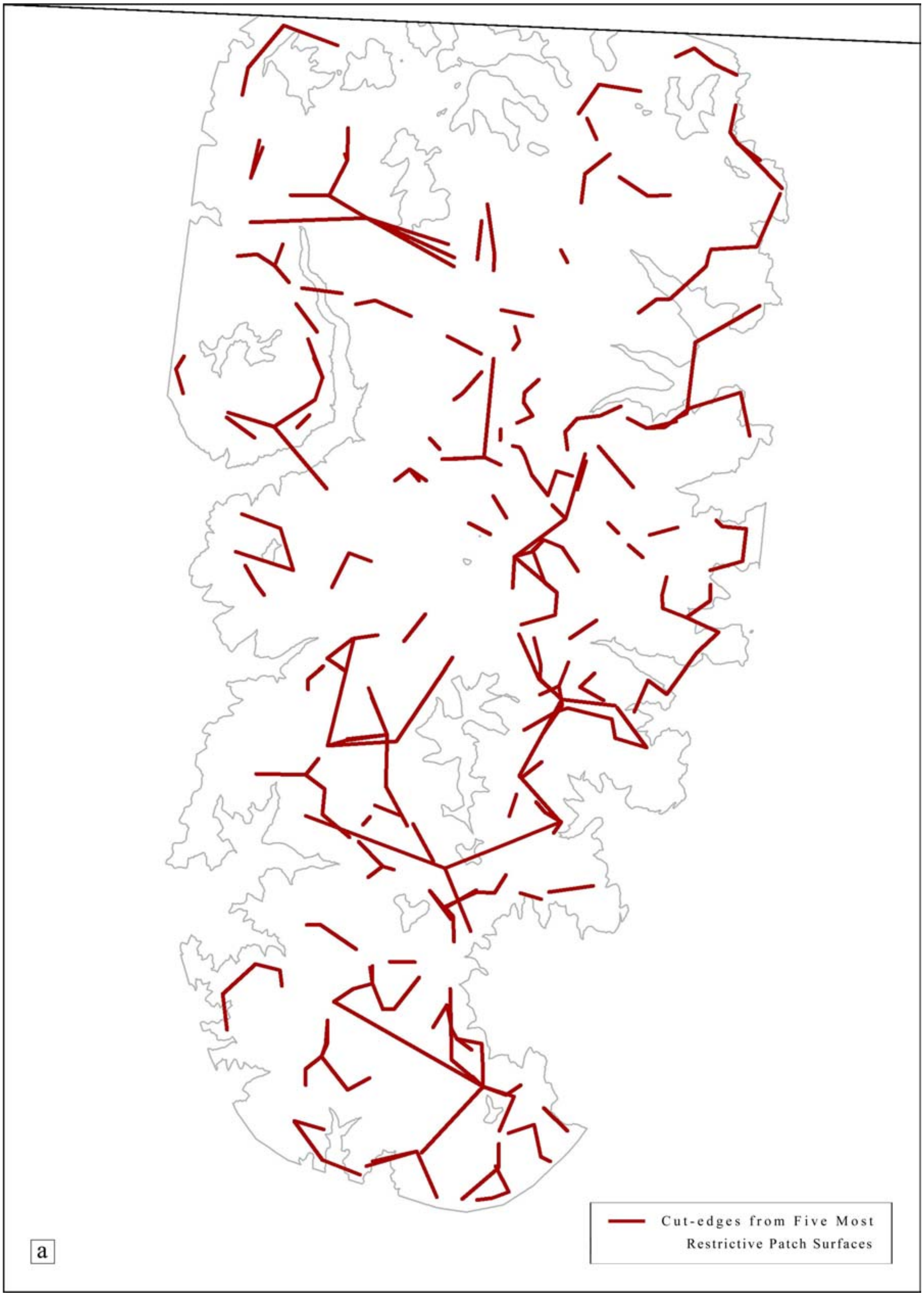


Figure 15a – Study-wide cut-edges

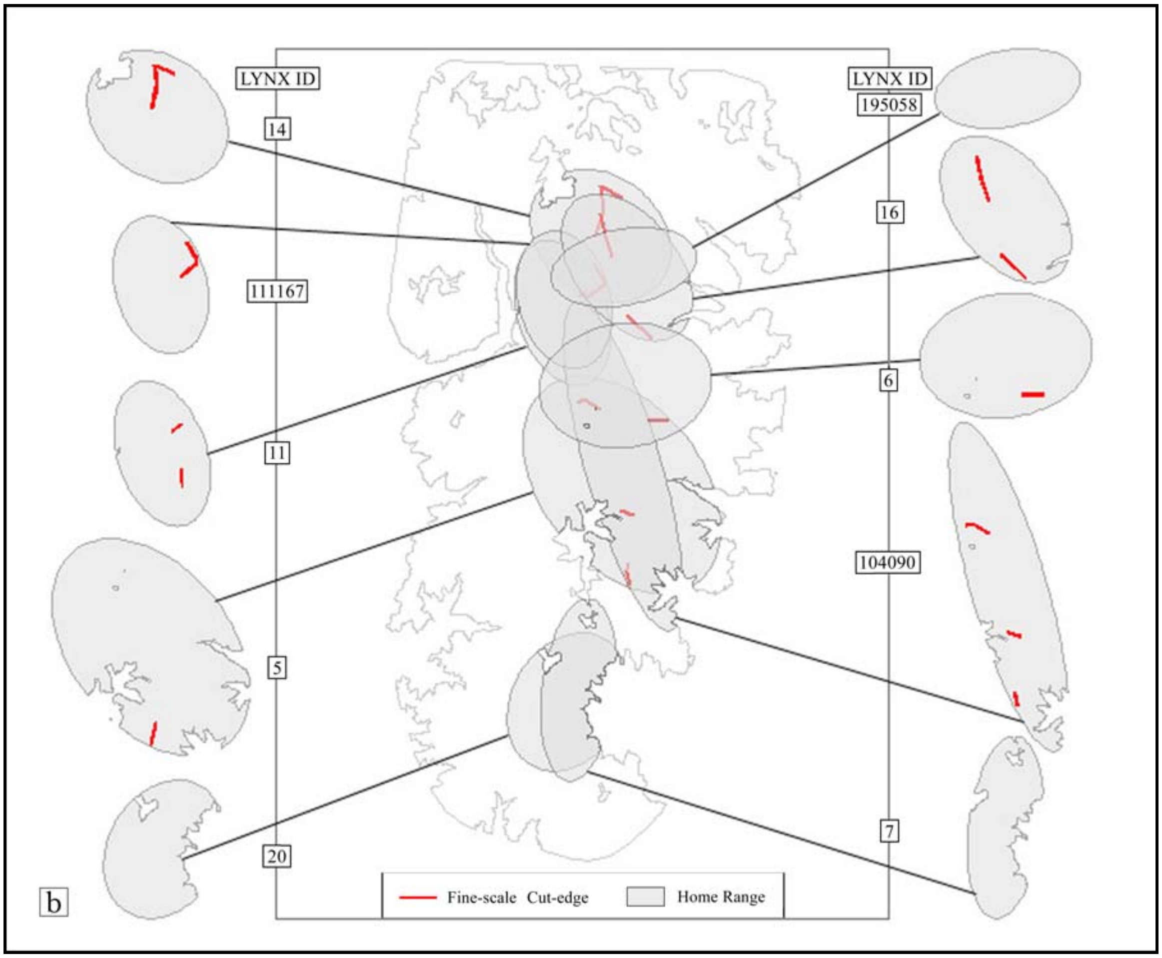


Figure 15b – Within-home-range cut-edges

Initially, two density surfaces were compared for MSTs – one for those originating from all ten patch surfaces (at area-of-presence thresholds 1%, 3%, ... , and 19%)(Figure 16a), and the other for only those MSTs generated from the five most restrictive patch surfaces (at area-of-presence thresholds 1%, 3%, ..., and 9%)(Figures 16b). Areas of high MST densities were largely coincident between the two density surfaces; specifically, the overlap composed 80.22% of high density areas in the former, and 71.41% of high density areas in the latter. The strength of this correlation provided justification for using only the density surface based on five MSTs and, secondly, for generating cut-edge densities only from those cut-edges identified in graphs based on the five most restrictive patch surfaces (Figures 16c).

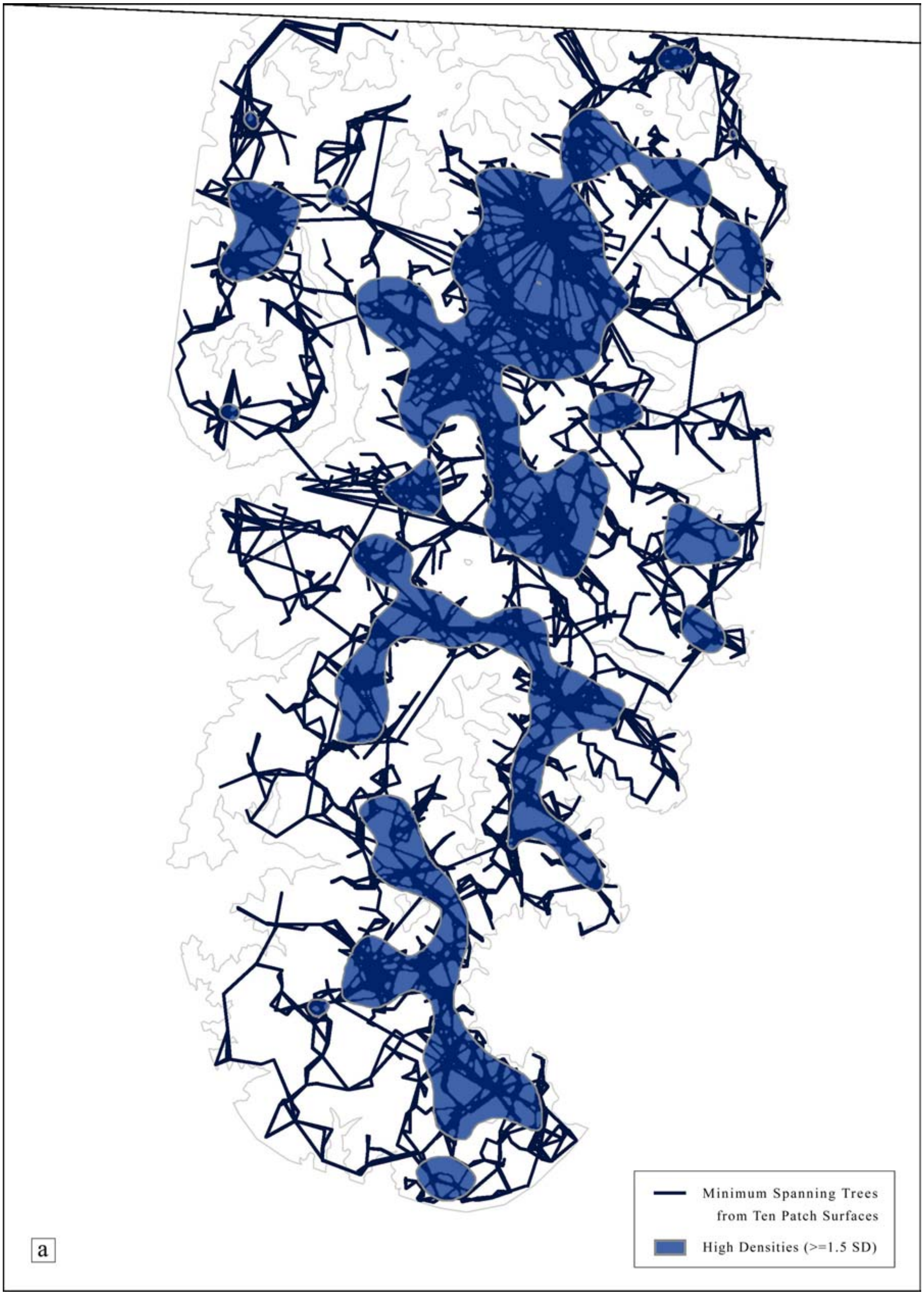


Figure 16a – High densities of the ten study-wide minimum spanning trees

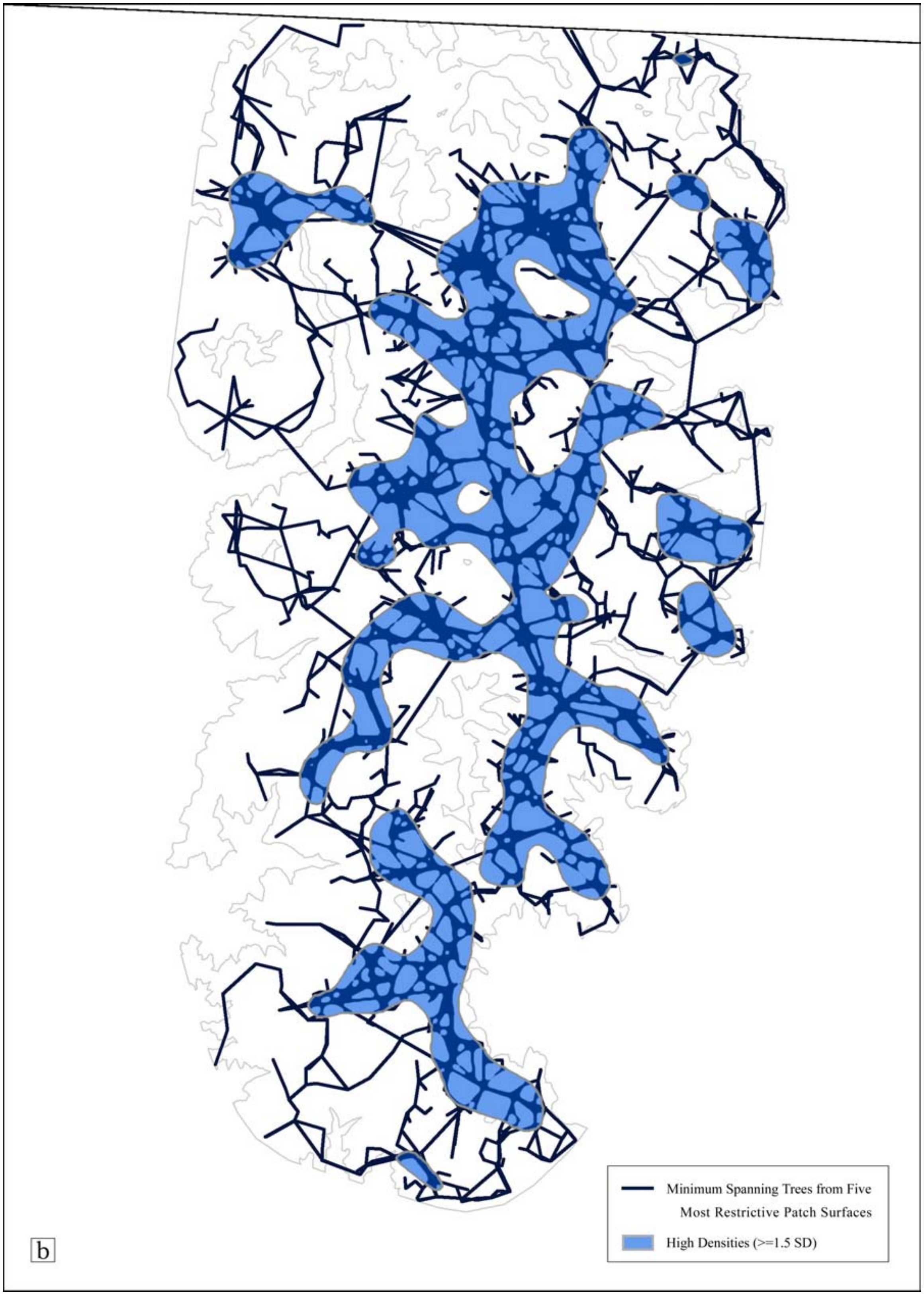


Figure 16b – High densities of the selected five study-wide minimum spanning trees

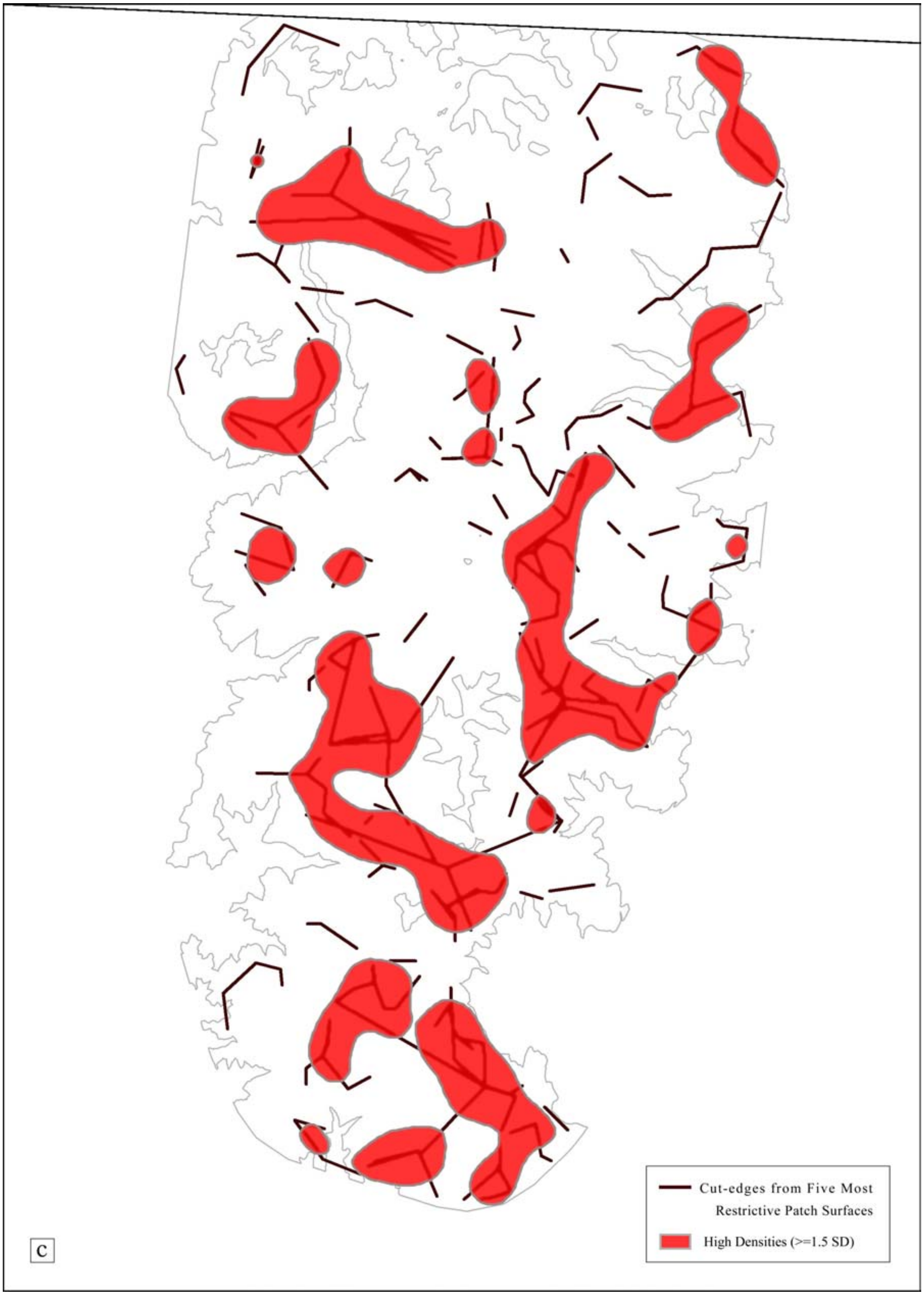


Figure 16c – High densities of study-wide cut-edges

RESULTS

With the exception of the habitat selection analyses considered prior to the designation of Bayes model inputs, the results from the two-phased modeling procedure correspond sequentially with the study objectives as previously set forth.

Study-wide Habitat Suitability

Comparative evaluation of the aggregate Bayes models was conducted in two respects. First, for each aggregate model, thresholds were defined at ten equal intervals in predicted suitability and the total areas above each were compared to areas of lynx presence in the corresponding test dataset. Second, each aggregate model, reclassified with class breaks set at these ten equal-interval thresholds, was cross tabulated against its corresponding test dataset with a χ^2 test of independence.

Of the three models, the one used as the basis for the cost surface, patch surfaces, and graph generation was derived from individual-based, multi-scale habitat selection analyses using the Jennrich-Turner home range estimator (i.e., selection scenario one). Against its corresponding test dataset, this surface predicted a higher percentage of known lynx presence at each of the decile suitability thresholds (Figure 17). Moreover, while χ^2 tests indicated that reclassed versions of all three models were able to discriminate between lynx presence and randomness at $\alpha = 0.02$, that of the chosen model resulted in the highest score of the three ($\chi^2 = 19.821$, df = 2, $p < 0.02$).

This final aggregate Bayes model represents lynx habitat suitability as predicated on probabilities of presence for any one of the ten most-sampled lynx (Figure 18).

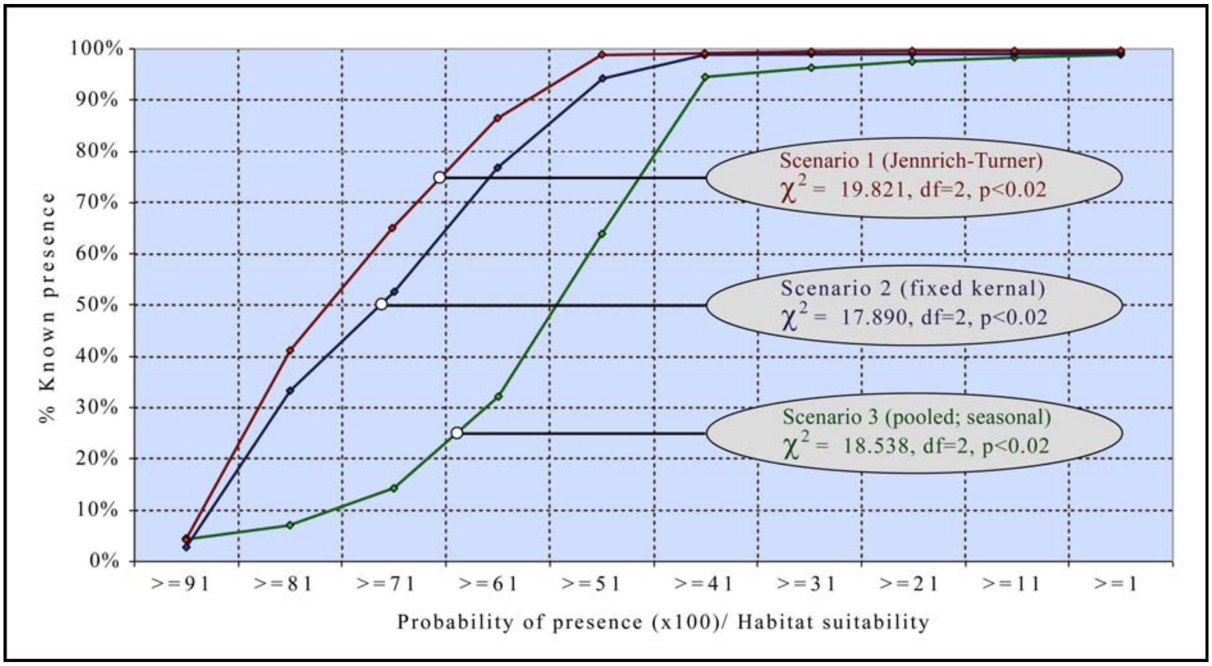


Figure 17 – Evaluation of the aggregate Bayes models

Study-wide Habitat Connectivity

Pattern recognition and quantitative indices can each facilitate comparative interpretation of overall habitat connectivity. For visual interpretation, the ten alternate study-wide graphs are juxtaposed in Figure 19. Each graph was also summarized by its number of components, its traversability, and its average connectivity. This provided quantitative measures of sensitivity to patch definitions (Figure 20).

Connectivity Hotspots

Mapping of edge densities provided composite representations of study-wide MSTs and cut-edges as they arose across variable patch definitions. Figures 21a and 21b compare the locations of high densities of each study-wide graph construct with its fine-scale counterpart.

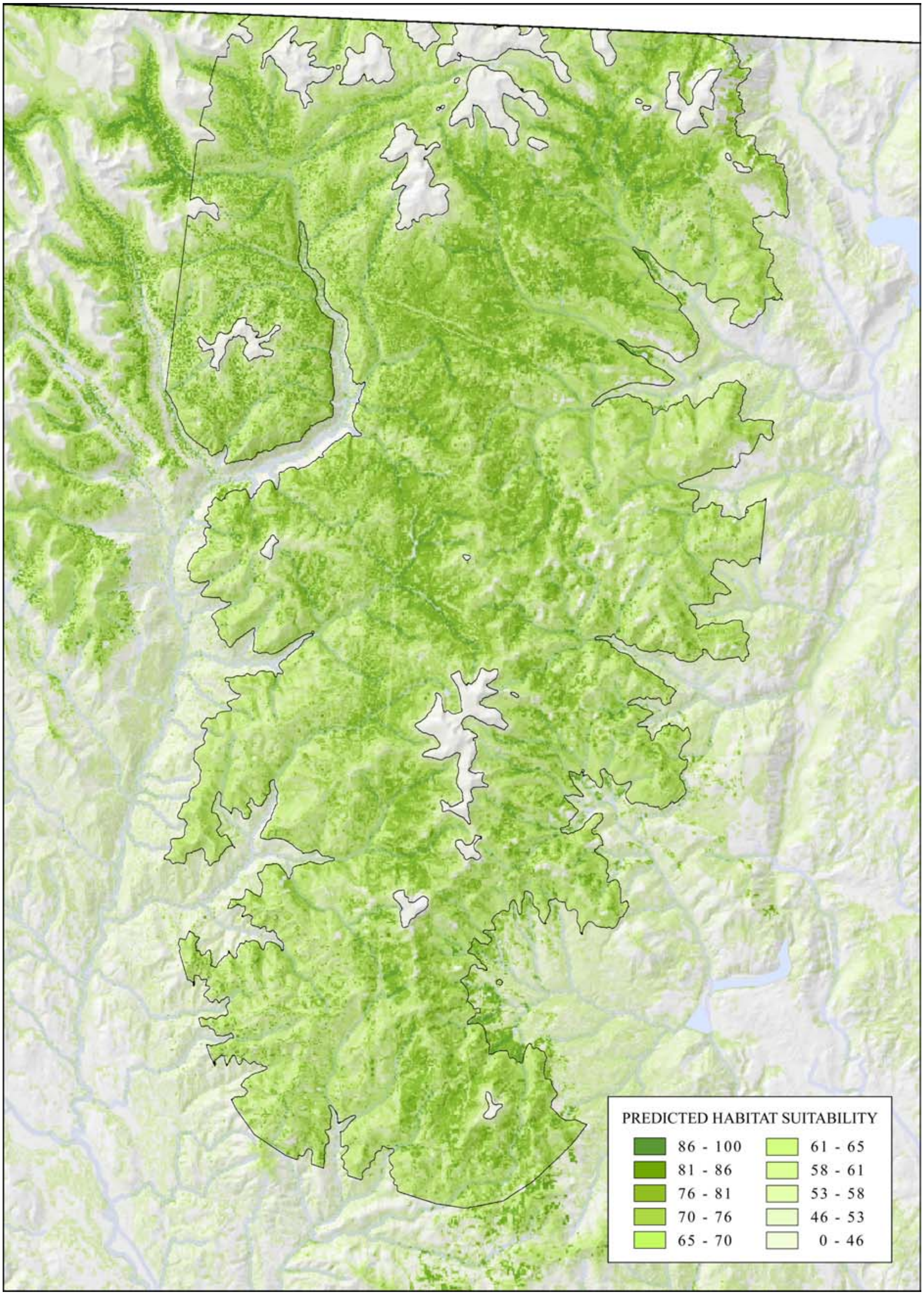


Figure 18 – The final habitat suitability map

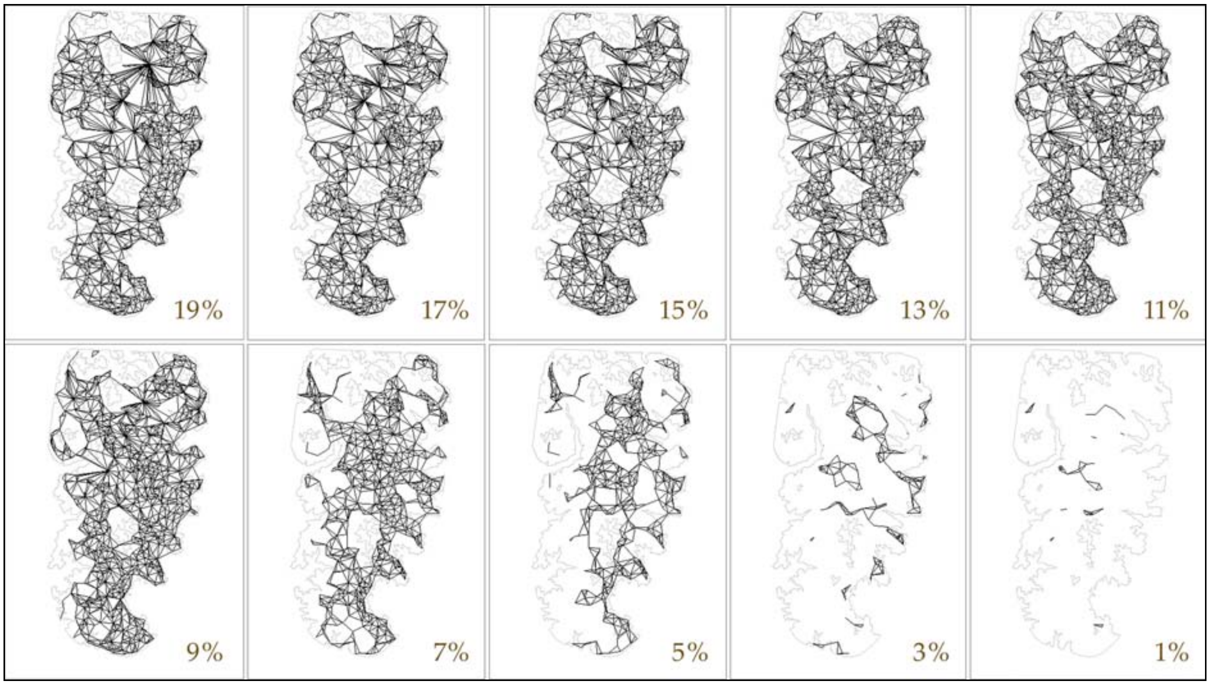


Figure 19 – Comparison of study-wide graphs based on the mean MDD

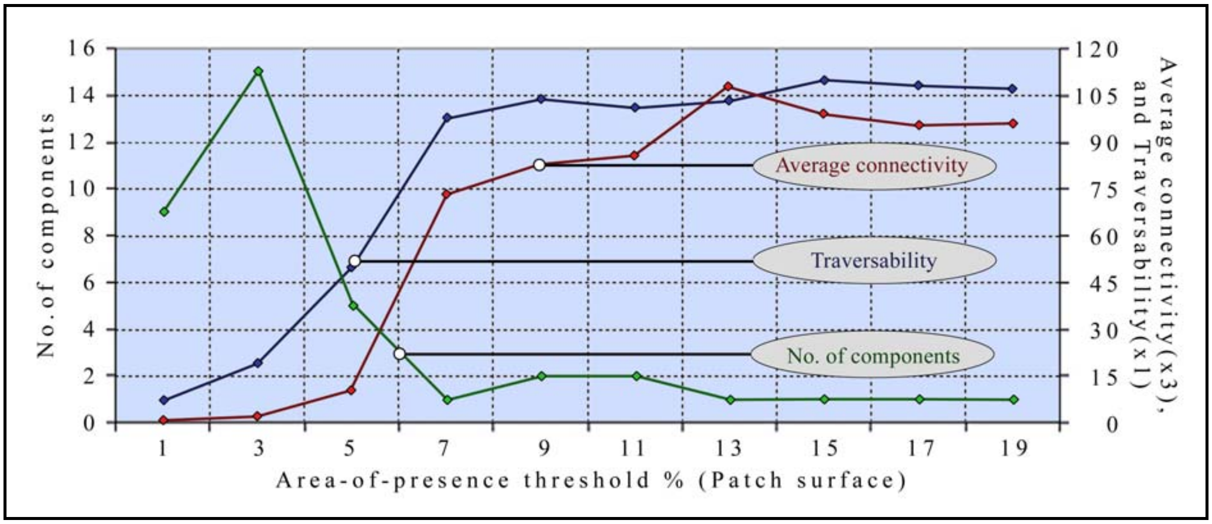


Figure 20 – Study-wide connectivity by selected metrics

To elucidate areas of higher conservation importance, the spatial co-occurrence between high MST densities and high cut-edge densities was mapped (Figure 22a). Each of these areas are indexed in Figure 22b and detailed in Figures 23a – 23h.

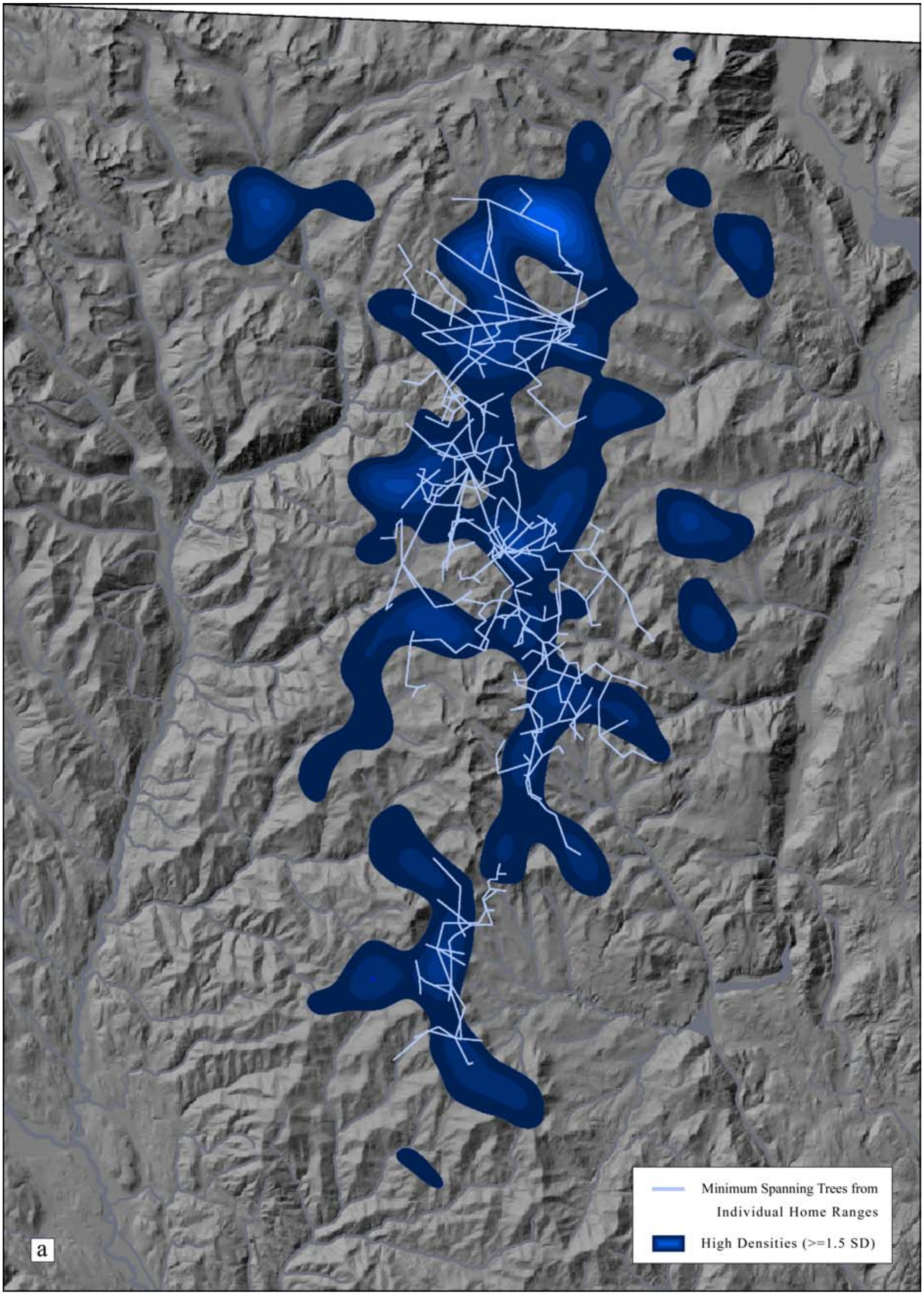


Figure 21a – High densities of study-wide MSTs compared with the ten fine-scale MSTs

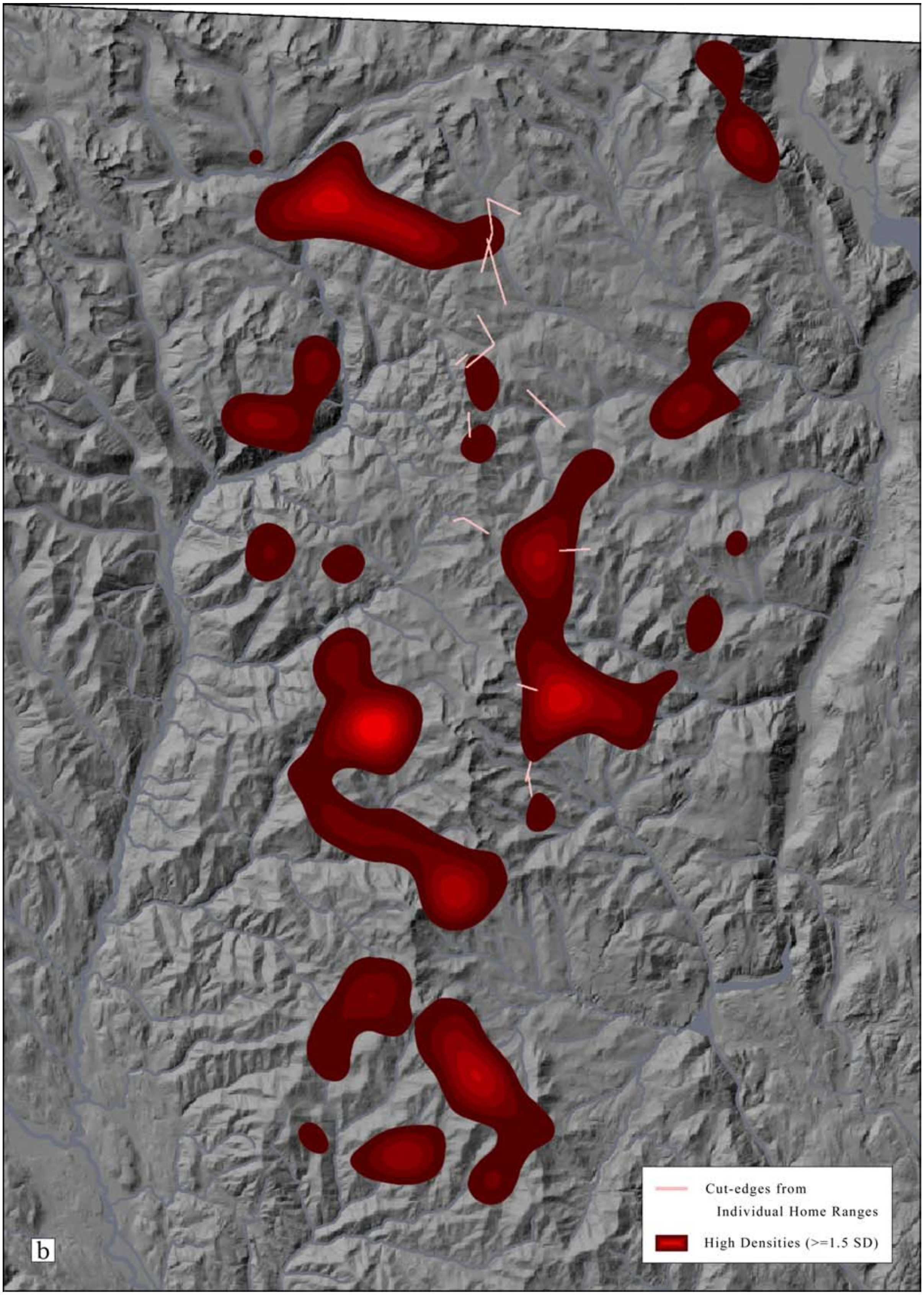


Figure 21b – High densities of study-wide cut-edges compared with fine-scale cut-edges

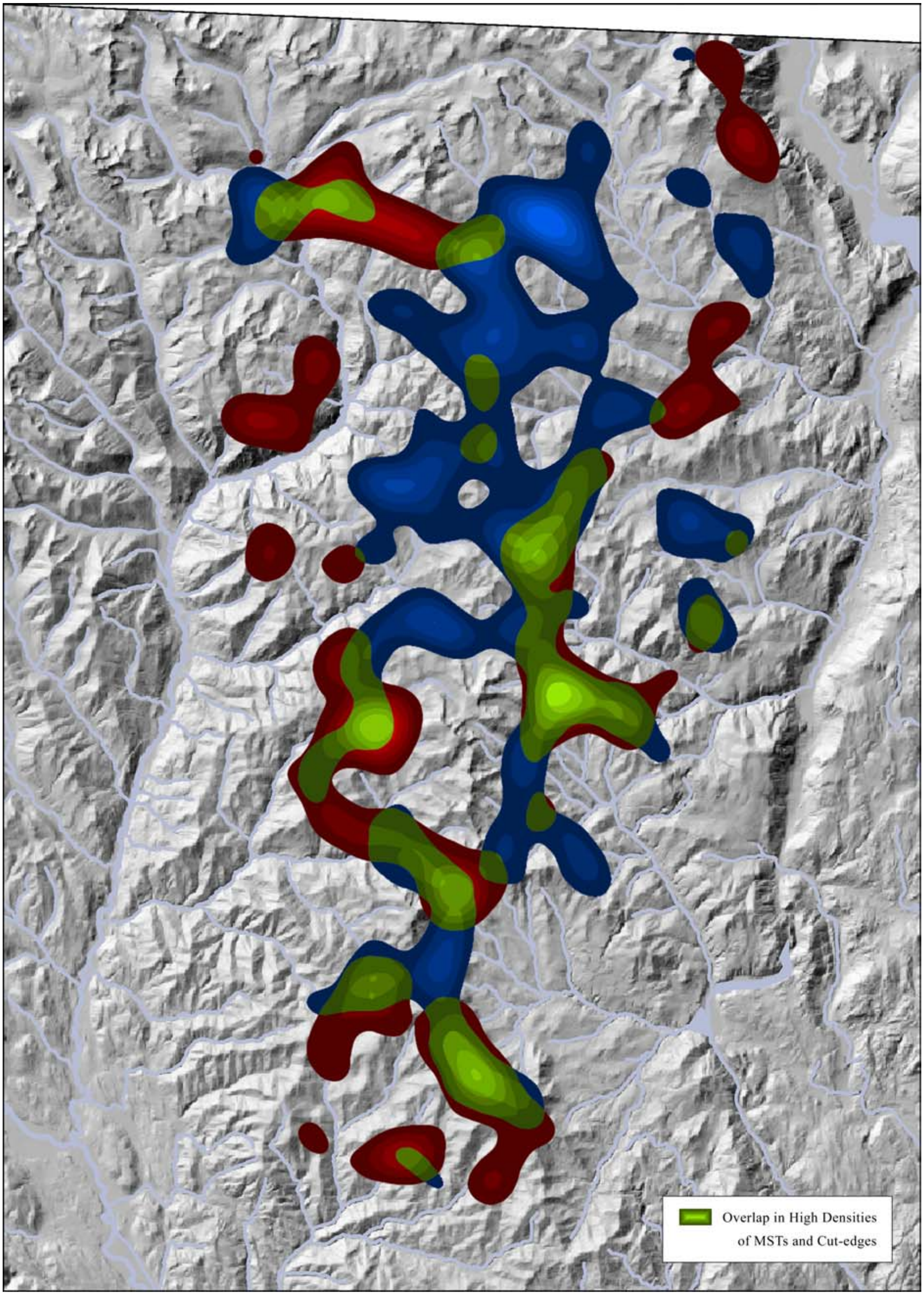


Figure 22a – Hotspots for study-wide connectivity

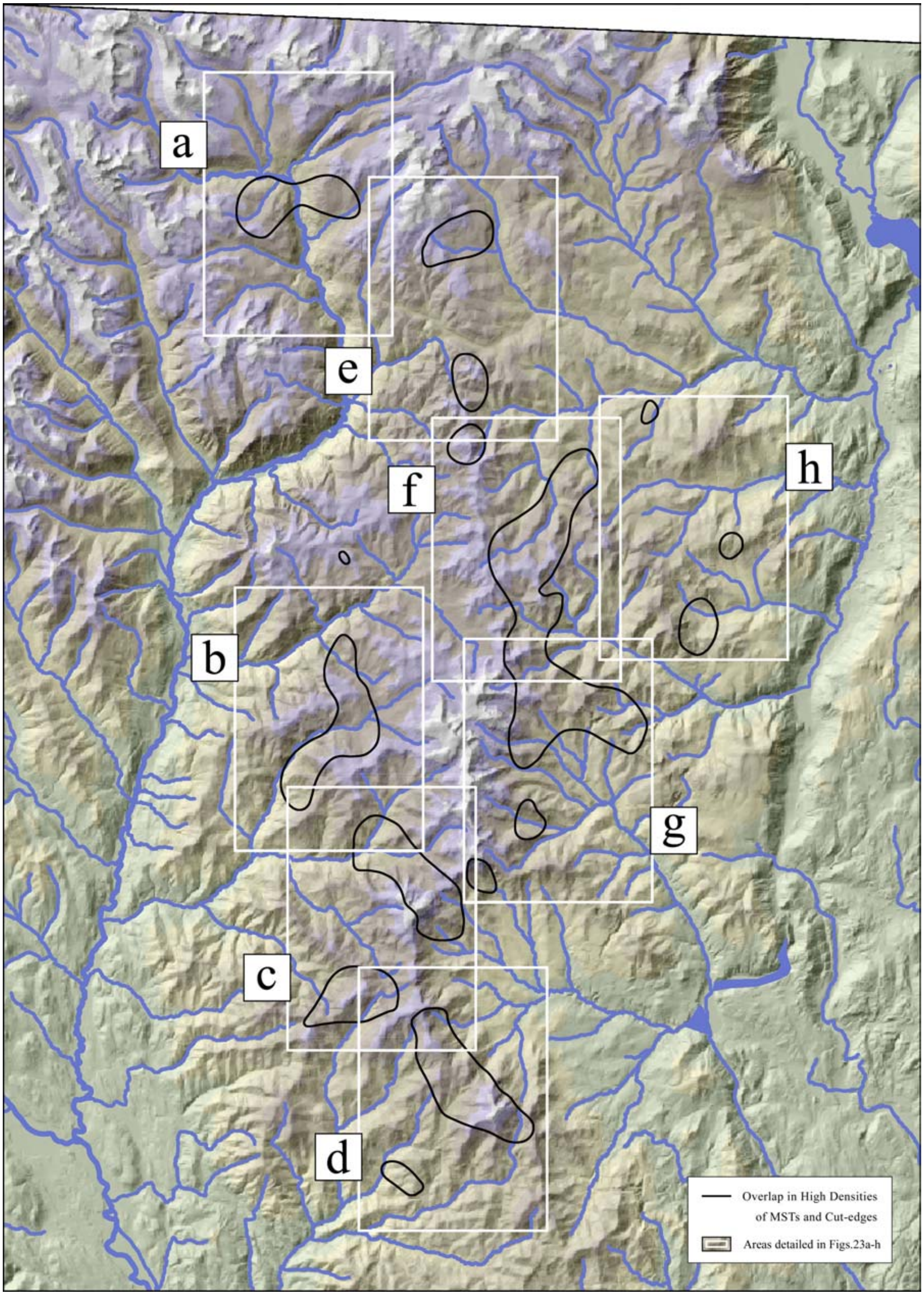


Figure 22b – Location map for Figures 23a – 23h

Beginning near the northwest bounds of the study area, the first area lies on the edge of the Pasayten Wilderness, bridging the Chewach River to include both the Wave Creek drainage and the south-facing slopes of the Basin Creek drainage (Figure 23a).

Further south along the western side of the study area, the next area covers the northwest-facing slopes of Spur Peak, the confluence of Brown Meadows Creek and the North Fork of Boulder Creek, and – extending to the north across the South Twentymile Trail – the middle sections of Timber Creek (Figure 23b).

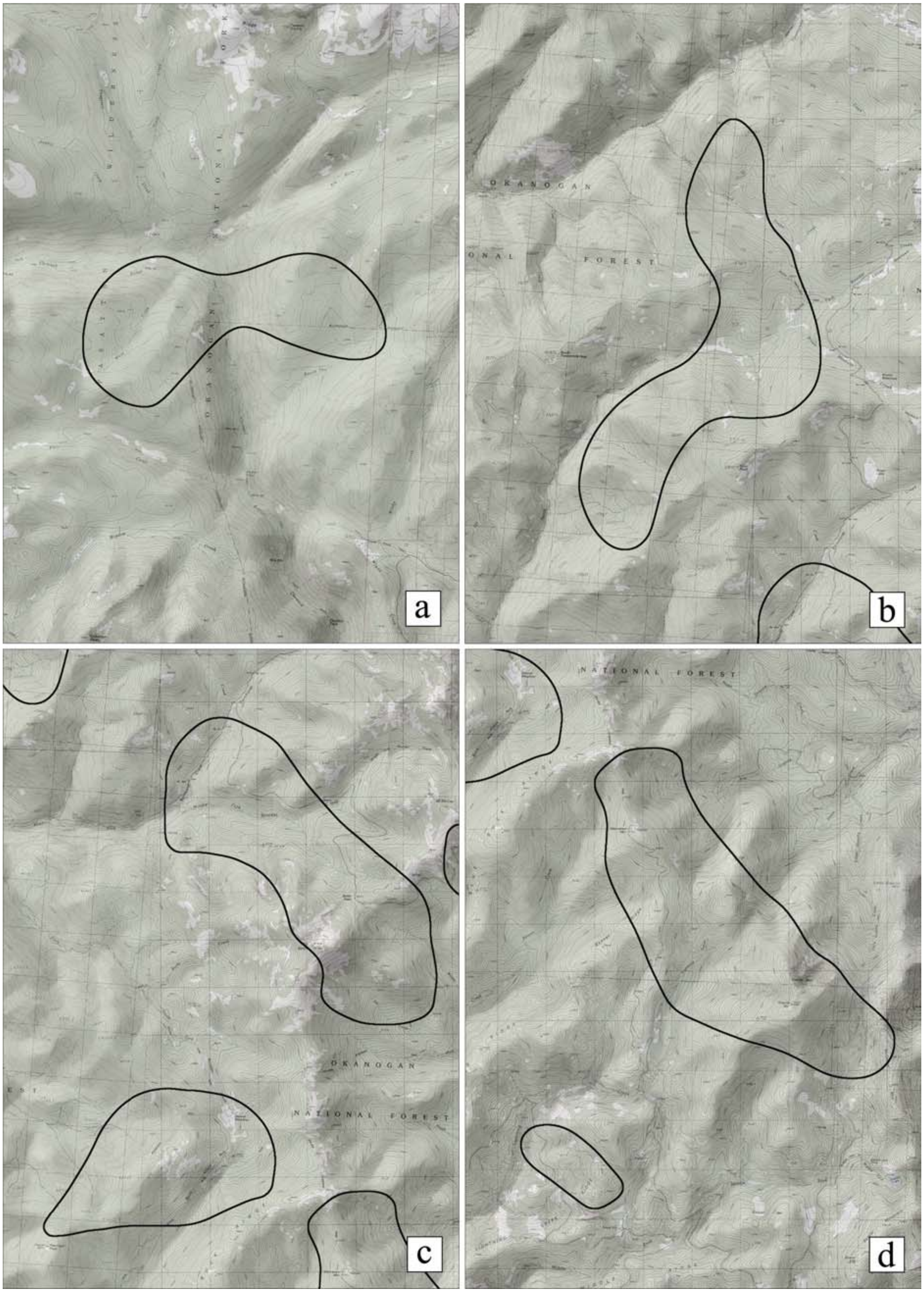
South of Spur Peak, a third area covers the confluence of Bernhardt Creek and the Middle Fork of Boulder Creek (Figure 23c). Extending to the southeast, it also includes Baldy Pass as well as Old Baldy itself and its southeast-facing slopes. Another area, southwest of Old Baldy, includes the confluence of Blue Buck Creek and the South Fork of Boulder Creek, and covers Beaver Meadows and the slopes northeast of Pearrygin Peak opposite Buck Ridge, including lower-elevation extents of Pearrygin, Blue Buck, and Golden Stairway Trails.

Southeast of Buck Ridge, the next area extends from Starvation Mountain and the upper-elevation stretches of the Golden Stairway Trail southeastward across the headwaters and upper reaches of Lightning Creek to include Granite Peak and its southeast-facing slopes (Figure 23d). South of this, another, smaller, area covers the west-facing slopes off the northern end of Lightning Creek Ridge.

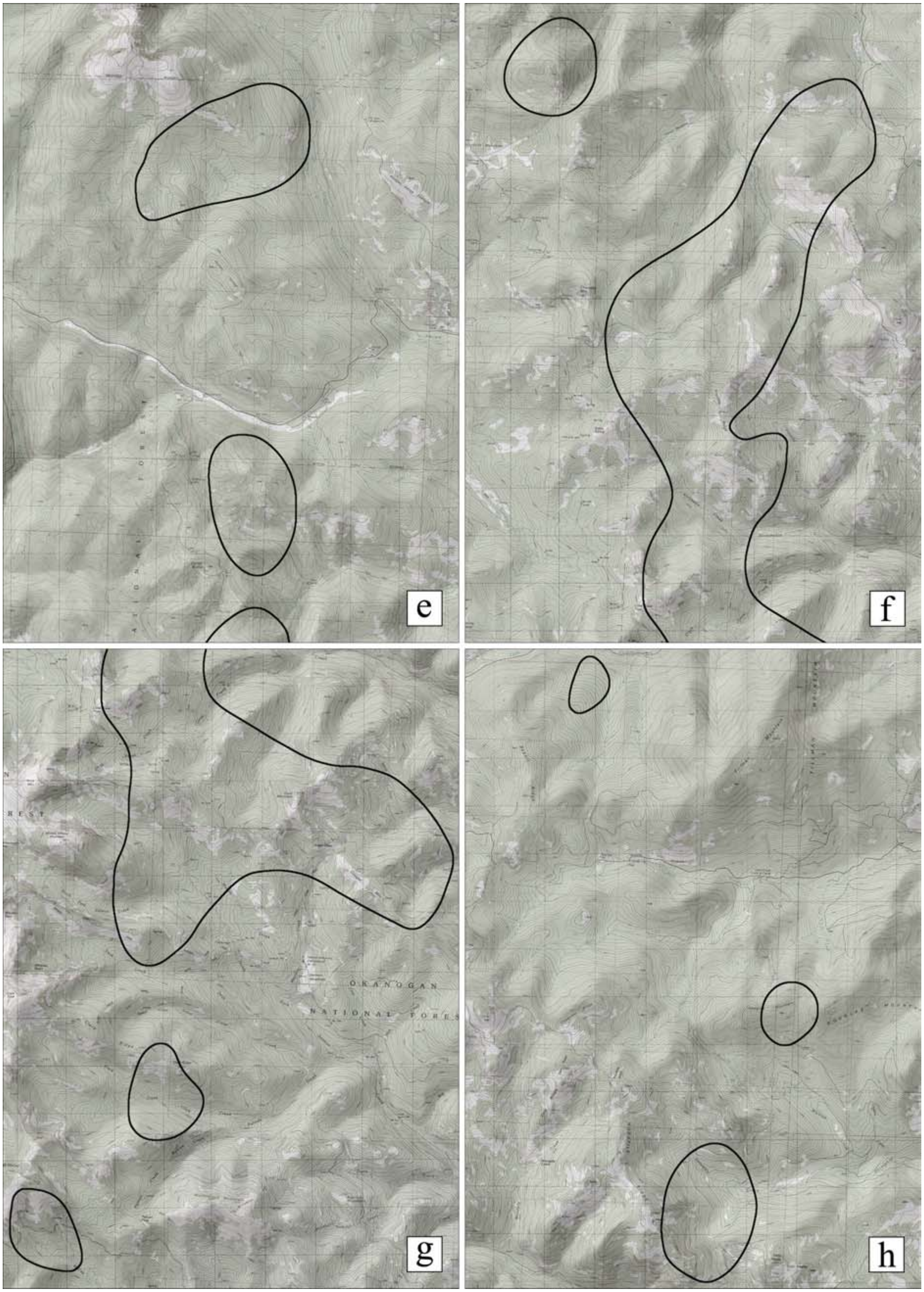
Again toward the north of the study area and adjacent the Pasayten Wilderness, the seventh area comprises lower elevations on the southeast-facing slopes of Windy Peak (Figure 23e). This includes most of the McDaniel Creek drainage above its confluence with the Middle Fork of Toats Coulee Creek and the middle sections of the Clutch Trail. Directly south across Long Swamp, a smaller area lies off Corral Butte to the northeast.

Again directly south of this, a limited area encircles the peak to the northeast above Thirtymile Meadows (Figure 23f). The following, tenth area is the largest of those mapped; this begins near the headwaters of Spring Creek and extends to the southwest to cover most of the drainage of the South Fork of Toats Coulee Creek (beneath Thunder Mountain to the west) and southward to include Timothy Ridge and much of the upper waters of Sinlahekin Creek. Continuing southward, the area includes most of the upper reaches of Lone Frank Creek, the east-facing slopes leading up to Rock Mountain and Middle Tiffany Mountain to the west, the mouth of the North Fork Salmon Creek drainage, and the headwaters of Mutton Creek (Figure 23g). Extending from here further to the southeast, it also includes Coxit Mountain, Angel Pass, the middle sections of the Angel Pass Trail, and Cougar Mountain. To the south and southwest of this, there are two additional areas: one runs from the eastern end of Clark Ridge southward crossing Clark Creek; the other lies southeast of Mt. McCay over the headwaters of McCay Creek.

Three remaining areas fall near the eastern edge of the study area within Loomis State Forest (Figure 23h): the first lies on the northeast-facing slopes of Rabbit Ridge above the South Fork of Toats Coulee Creek; the second spans the western ridge of Douglas Mountain (above Wickiup Creek to the south, Chickadee Creek to the northwest, and Three Forks Creek to the north); and the last covers the basin at the upper reaches of Sarsapkin Creek to the east of Woodpile Ridge and the northwest of Twin Peaks.



Figures 23a – 23d – Connectivity hotspots in detail



Figures 23e – 23h – Connectivity hotspots in detail (continued)

DISCUSSION

Summary of Results

In review, the individual Bayes models in this study were each predicated on selection analyses that varied by spatial scale (i.e., selection of home-ranges, or within them) and comprised different statistical methods (i.e., compositional analysis, χ^2, and Neu's method). The three aggregate Bayes models compared the use, through their respective model sets, of two alternate home-range estimators (Jennrich-Turner and fixed kernal) and pooling of radiolocation data by season. In the second modeling phase, graph data structures were used to analyze several aspects of habitat connectivity across multiple study-wide patch surfaces and within individual home ranges. Finally, hotspots for study-wide habitat connectivity were identified and described.

Individual-Based Habitat Selection

Significant habitat preferences by individual lynx are inherent within each respective (scale-specific) pair of individual-based Bayes models (see Appendix E). However, results from the resource selection analyses (see Appendix D) can also be examined separately to assess: (1) the extent of concurrence between results from the different analysis methods, (2) the effects of using alternate home range estimators upon detection of preferences (or, in the seasonal case, of pooling the telemetry data), (3) distinctions in habitat preferences between the meso- and fine-scales, and (4) the degree of individual variation (or, conversely, of commonalities between lynx) relative to selection for or avoidance of certain habitat types.

Study-wide Habitat Suitability

As noted, the final aggregate Bayes model is a surface with 10 m resolution comprising rescaled probabilities of presence for any one of the ten most-sampled lynx (Figure 18). Generated through an objective protocol, the surface is as an empirically based predictive map of relative lynx habitat suitability across the study area commensurate with the cumulative temporal relevance of the predictor datasets. At a glance, some marginal habitat is predicted at lower elevations, but the vast majority occurs (foreseeably) over the plateau of the Highlands and at higher elevations to the west and northwest. Much of the quality habitat appears in the northward core of the study area and in subalpine valleys in the Pasayten Wilderness, with the best areas occurring across the drainages for the North and Middle Forks of Toats Coulee Creek and, in the northwest, along the upper stretches of the Chewach River.

Study-wide Habitat Connectivity

The ability of graphs to support both visual and quantitative interpretation is particularly advantageous in the modeling of open, complex systems such as landscape mosaics. Visually, the study area appears well connected according to the less restrictive patch surfaces (at area-of-presence thresholds 11%, 13%, 15%, 17%, and 19%) (Figure 16). At the 7% area-of-presence threshold, however, peripheral areas are shown more tenuously connected. At the 5% threshold, the western side of the study area appears highly disconnected, while at the 3% and 1% thresholds, fragmentation is extensive across the entire plateau. The only area that appears consistently well connected across every patch surface runs, generally, from Thunder Mountain northwest and westward along the drainage for Thirtymile Creek.

The three connectivity metrics used - number of graph components, traversability, and average connectivity - corroborate what can be seen across the ten graphs. By each index, study-wide connectivity remains fairly constant across graphs derived over less restrictive patch surfaces (at area-of-presence thresholds 7%, 9%, ..., 19%). Connectivity begins to decline markedly, however, for graphs based on more restrictive patch surfaces (at area-of-presence thresholds 5%, 3%, and 1%). That each metric appears relatively insensitive to variable patch definition at and above the 7% area-of-presence threshold further supports the use of this threshold for defining fine-scale patches within specific home ranges.

Connectivity Hotspots

The locations of high densities for MSTs and cut-edges represent, respectively, the core "tissue" and the most vulnerable linkages in lynx habitat connectivity (Figures 21a and 21b). Areas of dense MSTs form a largely contiguous "meta-backbone" in itself, running north-south along the center of the plateau. High density areas for cut-edges are more diffuse, with more prevalence toward the peripheries of the study area. This divergence suggests that, in general, the "parsimoniously-connected" cores of lynx habitat may also be the areas most resilient to fragmentation.

Comparison of these surfaces with the fine-scale MSTs and cut-edges suggests areas that are simultaneously important to study-wide and within-home-range connectivity. Fine-scale MSTs are strongly coincident with high study-wide MST densities, while proportionally only a slight overlap is evident in the case of the cut-edges. The correlation in the instance of the MSTs is not immaterial. Nevertheless, the fine-scale graph constructs cannot be used as standards by which to assess the significance of the study-wide high-density areas, for, traced to their origins in the modeling process, the latter areas are derived from habitat selection at both meso- and fine-scales. Consequently, they constitute more holistic representations of connectivity than do the graph constructs for specific home ranges. Moreover, in that they were generated using multiple patch surfaces, the study-wide high-density areas are also more robust representations.

Conservation Implications

The habitat suitability and graph models herein are complementary in their capacities to help inform ongoing land management and conservation decisions affecting the resident lynx population. Whereas the suitability map can support efforts to identify and prioritize areas for protection (or restoration) with respect to relative habitat quality and patch-based metrics, the graphs can be used to expand the criteria for conservation priorities to include the influence of patch configuration upon lynx persistence.

Areas of high-densities in MSTs and cut-edges are those predicted to be of greatest importance to study-wide habitat connectivity. Each surface differs, however, in the justification it provides to conservation prioritizations. Because minimum spanning trees represent the parsimoniously connected backbones of connectivity, a concerted focus on their protection may be the most "efficient" way of preserving habitat connectivity. On the other hand, cut-edges represent areas by which connectivity is intrinsically most susceptible to disruption and for which the need for protection may be most imminent.

In light of the many interwoven considerations that shape effective conservation planning (e.g., prevention of habitat loss or degradation, mitigation for specific risk factors, opportunism, public support), it is valuable to know which areas merit the highest priority in the interest of maintaining lynx habitat connectivity over the Highlands. The areas of overlap between the two high density surfaces (Figures 22a, 22b, and 23a – 23h) are supported by both of the above arguments for protection and are thus most deserving of explicit concern.

Data Needs

Prior to the listing of lynx under the Endangered Species Act in March of 2000, Brittell et al. (1989) and Koehler (1990) constituted the most intensive and longest-duration efforts to document the spatial organization of a southern lynx population and, as a result, most information on lynx habitat relationships in the contiguous U.S. had, to that point, been derived from these two studies (McKelvey et al. 2000c). Any wildlife data (and especially that on rare carnivores) has its limitations, however, and those inherent to these telemetry data have led to two notable consequences for this study.

First – and likely owing to the unavailability of Global Positioning System technology at the time of the studies – temporal resolution and accuracy of the field data were not sufficient to support dynamic modeling. Because models in this study were static, they cannot reflect consequences of lynx demographics.

Second, because the source data were collected exclusively from resident lynx with established home ranges, detected selection patterns may reflect foraging, mate-finding, denning, or evasive activity, yet are unlikely to be indicative of exploratory movements. No exploratory movements were detected, for instance, in Koehler (1990). Furthermore, even while the confounding effects of immigration and emigration are avoided, results of selection analyses cannot be assumed to exemplify selection behavior that occurs during singular, long-range dispersal events. Similarly, because the study area was defined solely by radio-locations for these resident individuals, models were not of sufficient spatial extent to support consideration of metapopulation dynamics or exploration of possible linkages between proximate lynx populations. Considered as a measure of conservation potential, therefore, connectivity modeling in this case regards the effects of landscape configuration and spatial scale upon individual performance and survival, and not on population persistence or survivorship per se.

Of the many further modeling possibilities that additional data might support, several merit mention here. These include dynamic modeling of habitat connectivity, the addition of snowshoe hare densities and snow conditions as predictor datasets, the qualified extrapolation of the Bayes models to broader spatial extents, and the evaluation of the Bayes models against recent documentation of lynx presence across the study area.

With (2002) proposed that future dynamic habitat connectivity analyses be framed within the context of shifting landscape mosaics and disturbance architecture. Remote sensing data – abundant, readily available, and given to periodic updates – has greatly expedited analyses of landcover change and brings this prospect within nearer reach. Because habitat connectivity involves the interaction of species movement and landscape structure, optimally these efforts would hierarchically compare landcover change with species movement data across various temporal scales. However, as noted previously, movement data on carnivore species is exceptionally difficult to secure and is currently most often unavailable with the temporal intensity and duration necessary to support this component.

The candidate predictor variables used in this study were chosen in accord with two conditions: (1) evidence in the literature which supports their influence on habitat selection at subregional scales by either lynx or snowshoe hares, and (2) the availability of adequate datasets. While several of these variables were included by virtue of their supposed influence on snowshoe hare densities (i.e., stand structure and species group), others were regarded to function, in part, as surrogates for snow depths and hardness (i.e., the topographic variables, and canopy coverage). Nevertheless, had sufficient data been available for direct estimation of study-wide snowshoe hare densities or snow conditions, use of these predictors instead of their surrogates could potentially have enhanced model accuracy while reducing the total number of predictors and improving parsimony across the candidate set.

Spatial extrapolation of the Bayes models (and associated graphs) is an appealing notion given the supposed importance of lynx dispersal from the Canadian Rockies and northern taiga in augmenting southern populations (McKelvey et al. 2000; Mowat et al. 2000). Judging from the ten graphs based on interpatch cost distances set to the mean MDD of the sampled lynx (Figures 16 and 17), habitat within the study area appears relatively well-connected. However, the potential and requisite conditions for successful dispersal between lynx populations remains unknown (Ruggiero et al. 2000b).

Conceivably, the telemetry data supporting this study could be used to generate conditional probabilities for predictor datasets across a broader extent that might encompass potential inter-population linkages. This, however, would entail expansion of the “meso-scale” zone of availability beyond the scope supported by the data and, as a consequence, the resulting Bayes models would not necessarily reflect habitat selection behavior as manifest in the radiolocations. Nevertheless, extrapolation could prove to be a worthwhile exercise if additional test data existed for areas outlying the original study area and if interpretation of the expanded models was qualified by recognition of any significant physiographic differences in those areas.

Similar to the case for spatial extrapolation, it could be instructive to test the aggregate Bayes models against more recent location data within the study area itself. The landcover predictor datasets used for the models were classified from Landsat imagery that coincided with the timeframe of the two telemetry studies (1981-1988). Consequently, by virtue of both lynx presence data and predictors, the Bayes models are linked to the temporal context of those studies. However, this is not to suggest that the relevance of the models is necessarily outdated. While forest succession and other changes in the landscape mosaic have occurred in the time since, the relative import of those changes upon the relevance of the models can only be assessed through their evaluation against current presence data. Although unavailable for this study, locations for lynx and snowshoe hares in the study area have indeed been collected over recent years (G. Koehler, Research Scientist, Washington Department of Fish and Wildlife, 30 August 2002, e-mail).

On Risk Factors

On the ground, some lynx locations may have been directly or indirectly affected by factors in the landscape that, although generally "neutral" to selection behavior, may nonetheless effectively alter habitat quality by lowering the chances of an individual's survival. Such risk factors include interference and exploitative competition as well as markedly frequent or disruptive human activities.

It is conceivable that a set of candidate predictors might include layers representing the estimated home ranges of sympatric competitor species (e.g., cougars, coyotes, bobcats) or areas of permanent or otherwise intensive human activity (e.g., heavily traveled roads, active logging operations). However, in this study, the extent and frequency of locational displacement resulting from risk factors was assumed to be negligible when considered against the entire telemetry dataset. Consequently, radiolocations were assumed to be exclusively indicative of lynx habitat preference.

Rather than including risk factors in the generation of the Bayes models, it could be more sensible to regard them as means for the subsequent modification of either habitat suitability or impedance values. Individual cell values, that is, could be discriminately altered in accord with specific instances of risk. This would allow for the incorporation of isolated or clearly delimited features (e.g., roads or other human structures), relative weighting of those features (e.g., of roads by traffic volumes), and the incorporation of risk factors that may indirectly affect lynx productivity or mortality without necessarily influencing their behavior and locations (e.g., as hypothesized – increased presence of competitor species as a result of snow compaction from snowmobile use). Alternatively, weights based on risk factors could be applied to graph edges rather than to the interpatch cost surface(s).

Critique of Methods

Bayesian Habitat Modeling

Several aspects of the Bayesian procedure make it apposite for the prediction of species occurrence (or, habitat suitability). First, as an inductive method for pattern recognition (Aspinall 1992b), it is appropriate given the observational genesis of most ecological data; where empirical gaps in such data often prevent adequate estimation of key parameters for deductive methods (Turner et al. 2001), inductive methods can be based on limited data and optimize its use.

Second, Bayesian modeling involves a normative and rational means of generating predictions of species occurrence (or, habitat suitability) under conditions of uncertainty (Aspinall 1992b). Beyond the requisite care in initial selection of candidate explanatory datasets, no a priori relationships need be assumed between them and the species distribution to be modeled; rather, hypotheses concerning habitat associations are generated and tested as an inherent part of the procedure, with measures of statistical significance provided for relationships between each class of each predictor dataset and the species distribution. Once appropriate inputs are identified and conditional probabilities calculated, Bayes theorem combines the latter with relative, a priori probabilities for species presence/ absence (or, presence/ randomness), thereby inductively “learning” habitat relationships from the known instances of species presence with fewer implicit assumptions.

Third, the method provides an accommodating framework for predicting habitat suitability in which many environmental factors may be of interest. Multiple sets of continuous and categorical data can be combined into a single model output and assessments made of error propagation consequent on combinations of those predictor datasets (Aspinall 1992b). The procedure itself can also be readily implemented in the GISystems in which landscape and habitat analyses are often conducted.

The Combined Bayesian Graph-Theoretic Approach

For focal species-based modeling of habitat connectivity, the pairing of Bayesian and graph-theoretic techniques is a sensible strategy on several grounds.

An Empirical Basis for Cost Distances. Most importantly, the approach provides an empirical basis for the derivation of interpatch impedance values (i.e., relative resistance to movement – or, the inverse of habitat quality - in the intervening matrix). Most often to date, impedances in least-cost path models have been determined through expert opinion (Clevenger et al. 2002). By this method, resistance parameters for different habitat types are estimated in accord with what is known of a species' life history and habitat selection behavior. Expert judgment plays an integral and complementary role to modeling at the stage of on-the-ground conservation planning (Forman 2004). In the context of cost surface-based modeling, however, it is preferable to avoid subjective assignment of impedance values and rely, instead, directly upon empirical data from the target species. By doing so, modeled cost distances are guaranteed to reflect the focal species' experience with the particularities of one's study landscape.

Precedents in empirically derived impedances include Palomares et al. (2000) and Ferreras (2001), in which interpatch resistance parameters were generated directly from dispersal rates for endangered Iberian lynx, and Ricketts (2001), in which maximum likelihood was used to estimate relative impedances of habitat types for butterfly movement.

In the Bayesian graph-theoretic approach, graph nodes and topologies are determined entirely from the habitat suitability surface and this Bayes probability surface (or aggregate model thereof) is derived wholly from species distribution and environmental data. Consequently, every graph-based metric (e.g., traversability, average connectivity) and construct (e.g., minimum spanning trees, cut-edges) can be traced back to field data.

Practical Compatibility. Graph-theoretic network characterization constitutes an effective complement to Bayesian habitat modeling in operational terms.

The computational efficiency of graphs makes them ideal for comparative analyses of habitat patch configurations as they emerge over any series of Bayes models. Such a series might include suitability surfaces based on alternate predictor dataset combinations or frameworks for selection analyses. Or, with the periodic generation of Bayes models, graphs might be used to inform habitat conservation priorities on an iterative basis commensurate with the amount and quality of available presence/ absence data or with improved resolution or accuracy of environmental data. If, as in this study, variation in habitat quality is gradual and patches not easily resolved, graphs also readily facilitate comparative analysis of connectivity across alternate patch surfaces as systematically generated from a single Bayes model.

Graphs are also sufficiently versatile to allow for the open investigation of patch networks based on variously defined interpatch distances across a single Bayes surface. If, as in this study, distance-decay functions are used to define graph edges (i.e., node adjacencies), connectivity can be assessed based on species movement and gap-crossing capabilities. If area-weighted distances are used, the effects of patch size can also be integrated. Furthermore, provided sufficient population data exists to weight patches by their potential to act as source habitats, distances can be defined by dispersal fluxes, leading to the possible integration of metapopulation dynamics with landscape pattern as the grounds for process-based indices of habitat connectivity (Urban and Keitt 2001).

Applicability for Carnivore Species. Beyond the aforesaid advantages, the combined Bayesian graph-theoretic method appears well suited as one approach to the particular challenges of modeling habitat connectivity for far-ranging carnivores.

The basis in Bayesian inference allows suitability modeling to be applied across the broad geographic extents (Aspinall 1994) characteristic of carnivore movements. The inductive nature of the Bayesian procedure also enables empirical modeling of habitat quality even when presence data for carnivore species is limited. Thirdly, for species such as Canadian lynx for which data are especially few, the formalism of the Bayesian method in itself may be particularly judicious.

For connectivity analyses, graphs (by which bond- or site-percolation can be modeled) are, on the one hand, inherently appropriate for use at regional scales. Percolation theory performs best with binary habitat classifications (Wiens 1997), and it is at these scales where the distinction between protected habitat and developed or agricultural land is often relatively strong and the structure of functional habitat networks more characteristic of island-biogeographic and metapopulation-theoretic models.[24] Graphs also can support iterative exploration and meaningful representation of the topology of habitat networks even when data on species' dispersal capabilities or minimum patch size requirements are few and knowledge provisional (Urban and Keitt 2001).

CONCLUSION

Beyond predicting areas of exceptional importance to maintaining habitat connectivity for resident lynx on the Okanogan Highlands, this study has sought to demonstrate, in a more general sense, use of the combined Bayesian graph-theoretic modeling approach.

Whereas the application here entailed two scales of analysis and comparative use of alternative home range estimators, methods of resource selection analysis, habitat patch surfaces, and connectivity metrics, the essential methodology adopted is relatively straightforward. For those that would apply the approach in other instances, the following suggestions are offered for streamlining the overall procedure. Choice of a single home range estimator can be made on the basis of requisite sample size, the general pattern of spatial use by the target species, the accuracy required, and the acceptable degree of bias (see White and Garrott 1990). Of the methods for resource selection analysis used here, compositional analysis is recommended by virtue of its adherence to the unit-sum constraint (see Aebischer et al. 1993). Although multiple patch surfaces were used in response to gradual variation in habitat quality across the study area, studies involving a more pronounced distinction in suitable habitat may only require a single patch surface. In either case, the suitability thresholds by which patches are defined may be based on percentages in coinciding area of known species presence, as here, by any number of methods based on spatial autocorrelation (see Aspinall 1992), or in accord with a species' scale(s) of foraging behavior and minimum area requirements (see Addicott et al. 1987). Selection of one or more metrics for graph connectivity may depend on software availability or computational feasibility given the relative complexity of graphs generated. Vertex connectivity has been extensively studied and is one appropriate, if provisional, index (see Oellerman 1996). If used, care should be taken to note the locations of the associated cut-node(s), as they may occur at the periphery of an otherwise well-connected graph. For global measures of graph connectivity, this author would recommend the use of traversability and, if possible, average connectivity (see

Beineke et al. 2002). With respect to scales of analysis, two should be maintained at a minimum; provided sufficient data, however, at least three are preferable in order to allow, at a meso-scale, for the expression of mechanisms operating at one or more finer scales and the influence of broader-scale constraints.

Although the case study here was conducted at the scales of second- and third-order selection for a subpopulation of resident lynx, the Bayesian graph-theoretic approach is equally applicable across any range of scales and levels of landscape patchiness relevant to a given focal species, including those commensurate with first-order selection. Used to investigate functional habitat linkages at the metapopulation level for far-ranging carnivores or other umbrella species, it can contribute to proactive, multi-species conservation planning and wildland network design. In areas where network design is in its initial stages, graphs representations can serve as early indicators of areas functioning as habitat linkages for individual umbrella species or suites of selected species within "umbrella schemes". In cases where regional linkages have already been mapped, the method would be effective in supporting their iterative evaluation, prioritization, or refinement. The approach may be particularly instructive when applied at subregional scales over which dispersal events are still at question and yet where functional connectivity may rely on critical matrix habitat lying outside known core areas and corridors.

Irrespective of the scale(s) of application, an empirical basis for impedances addresses a key challenge in habitat connectivity modeling for focal species – that of assuring that linkages, as identified, are indicative of a species-centric perspective on the study landscape. In that all impedance values are tested against independent species presence data, the approach also represents a new, defensible way of evaluating the capacity of landscapes for supporting wildlife movement.

NOTES

1. Citing their own findings for pine marten (*Martes americana*), Bissonette et al. (1997) noted that although individual animals may not be physiologically capable of responding to scales broader than their home range at any given time, they may be aware of outlying habitat availability through exploratory movements or from juvenile dispersal.

2. During denning and parturition, an adult female's foraging movements may be less extensive though also, perhaps, more intensive out of the need to feed her kittens.

3. Maximum dispersal distances for lynx have been recorded at 1, 000 km (Mech 1980; Poole 1997b), as compared to 378 km for wolverine (*Gulo Gulo*) and 100 km for fisher (*Mustela pennanti*) (Craighead et al. 1999).

4. As a forest mesocarnivore, lynx are not an alpha predator, per se. However, they nevertheless are considered "top-level" predators and during periods of snowcover there would often appear to be sufficient spatial displacement with potential competitors to place lynx at the top of the food web at a local scale.

5. With the exception of compositional analysis and as otherwise specified in the Methods chapter, modeling procedures were conducted using ArcGIS 8.x and ArcView GIS 3.x (Environmental Systems Research Institute 1992-2003).

6. The relationship between landscape ecology and geography remains particularly strong today among Europeans, while in Britain in particular, the field is recognized to be largely the bailiwick of geographers (Haines-Young et al. 1993).

7. Quantitatively, Forman (1995) described the landscape-scale as that by which spatial elements on the landscape are discernible at one km^2 resolution.

8. With his proposed principles for reserve design, Diamond (1975) precipitated the so-named SLOSS (i.e., Single Large Or Several Small) debate, regarding the question of whether one large, connected reserve is more effective at preserving biodiversity than several small patches of equivalent total area. Following on nearly two decades of contention, the question is now widely considered to be conditional upon "…species and their dispersal abilities, environmental variation, characteristics of catastrophic events, and landscape opportunities that remain." (Breiniger et al. 2002, p.413). The longevity of the SLOSS debate stands as a testament to the theoretic import of MacArthur and Wilson's species-area curve and its derivations.

9. The ecological usage of "edge" (referring to a patch boundary) is not to be mistaken for the graph-theoretic usage of "edge" to denote node-to-node connections. Patch edge-to-edge measures of distances were used in this study instead of centroid-to-edge measures as they are more robust to spatial complexity (Crooks 2002). Even while patch edges are represented as discrete boundaries, the natural variation of habitat suitability in the intervening matrix is explicitly manifest in this derivation of functional interpatch distances and, thereby, a graph's topology.

10. For a description of several graph operations beyond edge-thresholding and their relevance for various types of conservation and land management decisions, see Urban and Keitt (2001).

11. Brittell et al. (1989) recorded 540 locations from 17 lynx; these were combined with 302 locations from 7 lynx gathered by Koehler (1990). Two individuals were monitored during both studies. Here, locations from these two lynx were analyzed separately respective to the study by which they were collected.

12. Red squirrels are known to be an important alternative prey species to snowshoe hare throughout the range of lynx, especially in the case of low hare densities in southern regions or during lows in their population cycle in the north (Ruggiero et al. 2000b). The dietary importance of red squirrels does not eclipse lynx reliance on hare, however; Koehler (1990) noted that a diet of red squirrels alone may not be sufficient to support lynx reproduction and kitten survival, while O'Donoghue et al. (1997) noted that lynx in southwestern Yukon appeared to capture red squirrels opportunistically when hares were abundant and to actively hunt them only when hares were scarce.

13. Beyond provision of thermal cover for kittens, adult lynx will presumably also adjust their movements out of their own need to thermoregulate, exhibiting a proclivity, for instance, for different topography or canopy closure based in part on thermal properties. There is some evidence for this in season-specific selection behavior in the Highlands study area — McKelvey et al. (2000c, p.334) found that, in summer, lynx exhibited a "more general use of cover types but consistently avoided warm, dry slopes..." Although this suggests thermoregulation was a driver of habitat preference in this case, seasonality may also be expressed through many other mechanisms. The season-specific resource selection analyses in this study were included to address this possibility.

14. Snow courses and SNOTEL (SNOwsurveyTELemetry) sites, each coordinated by the National Resources Conservation Service, provide the most extensive public domain archive of snow measurements in the U.S. Snow depth and snow water equivalent (SWE) readings are recorded monthly (usually January – April) at snow courses, while SNOTEL sites automatically record daily SWE, total precipitation, and air temperatures year-round. While SNOTEL data is far more frequent, fewer of these stations exist, such that the trade-off between data from either type of station is generally one between temporal and spatial resolution.

15. As modeled in a GIS, topographical complexity often involves some combination of profile and planform curvatures — respectively, the rate of change of slope and of aspect.

16. SWE measurements from the sole SNOTEL site in the study area were not necessarily representative of SWE across the plateau. They were used for estimating a functional distinction between seasons, however, because such a basis is, nevertheless, more specific to the study area than any *a priori* (e.g., equinoctial) designation of seasonality.

17. Files of the tests, including matrices of the compositional analyses, can be obtained by contacting the author via e-mail at: aaronjones@alumni.reed.edu

18. At any given point in time, the location of an animal may be indicative of its simultaneous selection for habitat across multiple spatial scales. For this reason, point-based definitions of lynx presence were sufficient for the evaluation of aggregate models derived from multi-scalar selection.

19. Movements by resident lynx outside the meso-scale zone of availability were assumed to be exploratory in nature and therefore more closely indicative of behavior during selection for a home range (i.e., dispersal behavior) than of activities within an established home range (e.g., foraging behavior). Although it has been assumed that lynx forage whenever they are traveling (Brand et al. 1976; Ward and Krebs 1985), here, such fine-scale selection behavior was assumed to be of secondary influence outside the meso-scale zone of availability; consequently, supplemental analyses used for extension of the original impedance surface were based exclusively on second-order selection.

20. As previously discussed, lynx are exceptionally motive and generally require large areas for persistence. More concerted estimation of minimum patch size requirements for the species, however, is a difficult affair; lynx habitat utilization is believed to be strongly influenced by snowshoe hare abundance (Ward and Krebs 1985; Breitenmoser and Slough 1993; Poole 1997a; Aubry et al. 2004) and habitat use distribution by hares appears highly variable, fluctuating in response to predatory pressures, browse availability, density dependence, and other factors (Hodges 2000a).

21. Throughout this study, the term "study-wide" is used in deliberate distinction from the term "meso-scale". While the latter refers to the bounds of the meso-scale zone of availability and associated selection behavior by lynx, the former refers to graph analyses and constructs occurring across the full extent of the final impedance surface and traceable to multi-scalar resource selection analyses.

22. Because an MST, by definition, must include every node (that is, without constraint on definition of node adjacencies by interpatch distance thresholds), and the set of all nodes remains constant between any one of the pre-graph networks and its derivative graph(s), MSTs can be identified directly from these networks as they would be identical to those for respective graphs.

23. If, as in this study, nodes are the centroids of habitat patches, then variable patch definitions – in addition to affecting the number of patches and nodes between patch surfaces – will also affect patch size and shape, and consequently, exact node placement. With differing patch definitions, edges, as well, are subject to some displacement in accord with the spatial shifting of nodes.

24. Granted, when functional interpatch distances are calculated to incorporate variable habitat quality in the matrix, the extreme simplification of binary habitat classification is avoided outright. Nonetheless, graph nodes must be predicated on habitat patches that are defined by set thresholds, and these thresholds are more easily distinguished within landscape patterns at regional scales.

REFERENCES CITED

Addicot, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., and Soluk, D. A. 1987. Ecological neighborhoods – scaling environmental patterns. *Oikos* 49: 340-6.

Aebischer, N. J., Robertson, P. A., and Kenward, R. E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74 (5): 1313-25.

Agee, J. K. and Kertis, J. 1987. Forest types of the North Cascades National Park Service Complex. *Canadian Journal of Botany* 65: 1520-30.

Agee, J. K. 2000. Disturbance ecology of North American boreal forests and associated northern/ mixed subalpine forests. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 3. Boulder, CO: University Press of Colorado.

Allen, T. F. H. and Starr, T. B. *Hierarchy – Perspectives for Ecological Complexity*. Chicago, IL: University of Chicago Press.

Alldredge, J. R. and Ratti, J. T. 1986. Comparison of some statistical techniques for analysis of resources selection. *Journal of Wildlife Management* 50(1): 157-65.

Alldredge, J. R. and Ratti, J. T. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56(1): 1-9.

Alldredge, J. R., Thomas, D. L., and McDonald, L. L. 1998. Survey and comparison of methods for study of resource selection. *Journal of Agricultural, Biological, and Environmental Statistics* 3(3): 237-53.

Anderson, G.S. and Danielson, B. J. 1997. The Effects of landscape composition and physiognomy on metapopulation size – the role of corridors. *Landscape Ecology* 12(5): 261-71.

Andrén, H. and Delin, A. 1994. Habitat selection in the Eurasian red squirrel, Sciurus Vulgaris, in relation to forest fragmentation. *Oikos* 70(1): 43-8.

Apps, C. 1998. East Kootenay Lynx Project: Lynx habitat selection and suitability in the southern Canadian Rocky Mountains. Annual Summary Report, Year 2, 1997-8. Calgary, AB: Aspen Wildlife Research.

———. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains – a study. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 12. Boulder, CO: University Press of Colorado.

Aspinall, R. J. 1992a. An Inductive modelling procedure based on Bayes' theorem for analysis of pattern in spatial data. *International Journal of Geographical Information Systems* 6: 105-21.

———. 1992b. Spatial analysis of wildlife distribution and habitat in a GIS. Charleston, SC: Proceedings of the 5th International Symposium on Spatial Data Handling.

———. 1994. Exploratory spatial analysis in GIS – generating geographical hypotheses from spatial data. In *Innovations in GIS 1*, ed. Worboys, M. F., pp. 139-48. London, U.K.: Taylor-Francis.

———. 2000. Bayesian modeling with ArcView GIS. Kalispell, MT: The GeoSpatial New West Intermountain GIS Conference.

Aspinall, R. J. and Veitch, N. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in a GIS. *Photogrammetric Engineering and Remote Sensing* 59: 537-43.

Aubry, K. B., Koehler, G. M., and Squires, J. R. 1999. Ecology of Canada lynx in southern boreal forests. In *The scientific basis for conserving forest carnivores – American marten, fisher, lynx and wolverine in the western United States*, eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Lyon, L. J. and Zielinski, W. J., pp. 74-98. RMRS-GTR RM-254. Fort Collins, CO: USDA Forest Service.

Aubry, K. B., Koehler, G. M., and Squires, J. R. 2000. Ecology of Canada lynx in southern boreal forests. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 13. Boulder, CO: University Press of Colorado.

Aubry, K. B., von Kienast, J., and Koehler, G. M. 2004. Influence of snow conditions on habitat selection by lynx in northern Washington. In *Conference proceedings of Carnivores 2004 – Expanding Partnerships in Carnivore Conservation*, p.17. Sante Fe, NM: Defenders of Wildlife, 14-17 November.

Augustin, N. H., Mugglestone, M. A., and Buckland, S. T. 1996. An Autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* 33: 339-47.

Bak, P. and Chen, K. 1991. Self-organized criticality. *Scientific American* 264(1): 46-53.

Beineke, L. W., Oellermann. O. R., and Pippert, R. E. 2002. The Average connectivity of a graph. *Discrete Mathematics* 252: 31-45.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7: 94-108.

———. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management*, 59: 228-37.

———. 1996. Metapopulation models, tenacious tracking, and cougar conservation. In *Metapopulations and Wildlife Conservation*, ed. McCullough, D. R., pp. 293-323. Washington, DC: Island Press.

Beier, P. and Noss, R. F. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12: 1241-52.

Bennett, A. F. 1999. Linkages in the landscape – the role of corridors and connectivity in wildlife conservation. Gland, Switzerland and Cambridge, U.K.: The World Conservation Union (IUCN) Forest Conservation Programme.

Bissonette, J. A. 1997. Scale-Sensitive ecological properties – historical context, current meaning. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J. A., Chapter 1. New York: Springer-Verlag.

Bissonette, J. A., Harrison, D. J., Hargis, C. D., and Chapin, T. G. 1997. The Influence of spatial scale on scale-sensitive properties in habitat selection by American marten. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J.A., Chapter 15. New York: Springer-Verlag.

Boutin, S., B. Gilbert, S., Krebs, C. J., Sinclair, A. R. E., and Smith, J. N. M. 1985. The Role of dispersal in the population dynamics of snowshoe hares. *Canadian Journal of Zoology* 63: 106-15.

Brand, C. J., Keith, L. B., and Fischer, C. A. Lynx responses to changing snowshoe hare densities in central Alberta. *Journal of Wildlife Management* 40(3): 416-28.

Breiniger, D. R., Burgman, M. A., Akcakaya, H. R., and O'Connell, M. A. 2002. Use of metapopulation models in conservation planning. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 22. New York, NY: Springer-Verlag.

Breitenmoser, U., and Slough, B. G. 1993. Predators of cyclic prey – Is the Canada lynx victim or profiteer of the snowshoe hare cycle? *Oikos* 66: 551-4.

Brittell, J. D., Poelker, R. J., Sweeney, S. J., and Koehler, G. M. 1989. *Native cats of Washington*. Unpublished. Olympia, WA: Washington Department of Wildlife.

Brown, J. H. and Lomolino, M. V. 1998. *Biogeography*, 2nd Edition. Sunderland, MA: Sinauer Associates, Inc. Publishers.

Bunn, A. G., Urban, D. L., and Keitt, T. H. 2000. Landscape connectivity – a conservation application of graph theory. *Journal of Environmental Management* 59: 265-78.

Buskirk, S. W., Ruggiero, L. F., Krebs, C. J. 2000a. Habitat fragmentation and interspecific competition: implications for lynx conservation. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 4. Boulder, CO: University Press of Colorado.

Buskirk, S. W., Ruggiero, L. F., Aubry, K. B., Pearson, D. E., Squires J. R., and McKelvey, K. S. 2000b. Comparative ecology of lynx in North America. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 14. Boulder, CO: University Press of Colorado.

Burrough, P. A., and McDonnell, R. A., 1998, *Principles of Geographic Information Systems*. New York: Oxford University Press.

Byrne, G. 1998. *A Colorado winter track survey for snowshoe hares and other species*. Unpublished report. Colorado Division of Wildlife.

Cantwell, M. D., and Forman, R. T. T. 1993. Landscape graphs – ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecology* 8(4): 239-55.

Carroll, C. 2000. *Spatial Modeling of Carnivore Distribution and Viability*. PhD. Dissertation. Oregon State University.

Carroll, C., Paquet, P. C., and Noss, R. F. 1999. *Modeling carnivore habitat in the Rocky Mountain region – a literature review and suggested strategy*. Report prepared for the World Wildlife Fund-Canada. Corvallis, OR: Conservation Biology Institute.

Clark, J. D., Dunn, J. E., and Smith, K. G. 1993. A Multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57(3): 519-526.

Clevenger, A. P., Wierzchowski, J., Chruszcz, B., and Gunson, K. 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* 16(2): 503-14.

Craighead, F. L., Gilpin, M. E., and Vyse, E. R. 1999. Genetic considerations for carnivore conservation in the Greater Yellowstone ecosystem. In *Carnivores in Ecosystems – The Yellowstone Experience*, eds. Clark, T.W. Curlee, A.P., Minta, S.C., and Kareiva, P. M., pp. 285–322. New Haven: Yale University Press.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16(2): 488-502.

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563-6.

Delcourt, H. R. and Delcourt, P. A. 1988. Quarternary landscape ecology – relevant scales in space and time. *Landscape Ecology* 2: 23-44.

Desrochers, A. and Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11(5): 1204-10.

Diamond, J. M. 1975. The Island dilemma – lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7: 129-46.

Diamond, J. M. and May, R. M. 1976. Island biogeography and the design of nature reserves. In *Theoretical Ecology – Principles and Applications,* ed. May, R. M., pp. 163-86. London, U.K.: Blackwell.

Dunning, J. B., Stewart, J. B., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H., and Stevens, E. E. 1995a. Spatially-explicit population models – Current forms and future uses. *Ecological Applications* 5(1): 3-11.

Dunning, J. B. Jr., Borgella, Jr., R., Clements, K., and Meffe, G. K. 1995b. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9(3): 542-50.

Environmental Systems Research Institute (ESRI), ArcView 3.x and ArcGIS 8.x, Redlands, CA (1992-2003).

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology* 66: 1762-8.

Farnes, P., Heydon, C., and Hansen, K. 1999. Snowpack distribution in Yellowstone National Park, Final Report, Proposal No.97-447, Cooperative Agreement Number CA 1268-1-9017, Grant and Contract No.291601, To J. Varley, Director, Yellowstone Center for Resources, National Park Service, Yellowstone National Park, WY 82190.

Ferreras, P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation* 100(1): 125-36.

Forman, D. 2004. *Rewilding North America*. Washington, DC: Island Press.

Forman, R. T. T. 1995. *Land Mosaics*. Cambridge, U.K.: Cambridge University Press.

Forman, R. T. T. and Godron, M. 1986. *Landscape Ecology*. New York, NY: John Wiley & Sons.

Foulds, L. R. 1992. Graph Theory Applications. New York: Springer-Verlag.

Fox, J. F. 1978. Forest fires and the snowshoe hare-Canada lynx cycle. *Oecologia* 31: 349-74.

Freemark, K., Bert D., and Villard, M. 2002. Patch-, landscape-, and regional-scale effects on biota. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 5. New York, NY: Springer-Verlag.

Gardner, R. H., Milne, B. T., Turner, M. G., and O'Neill, R. V. 1987. Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology* 1: 19-28, s3.

Garshelis, D. L. 2000. Delusions in habitat evaluation – Measuring use, selection, and importance. In *Research Techniques in Animal Ecology,* eds. Boitani , L. and Fuller, T. K., pp.111-64. New York: Columbia University Press.

Gross, J. T. and Yellen, J. 1999. *Graph Theory and Its Applications*. Boca Raton, FL: CRC Press.

Gross, J. T. and Yellen, J. 2004. *Handbook of Graph Theory*. Boca Raton, FL: CRC Press.

Grumbacher, S. K., McEwen, K. M., Halverson, D. A., Jacobs, D. T., and Lindner, J. 1993. Self-organized criticality – an experiment with sandpiles. *American Journal of Physics* 61(4): 329-335.

Grumbine, R. E. 1994. What is ecosystem management?: *Conservation Biology* 8(1): 27-38.

Gustafson, E. J. 1998. Quantifying landscape pattern – What is the state of the art? *Ecosystems* 1: 143-56.

Gustafson, E. J. and Gardner, R. H. 1996. The Effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94-107.

Gutzwiller, K. J. 2002. Spatial factors affecting organism occurrence, movement, and conservation – Introduction to Section II. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 4. New York, NY: Springer-Verlag.

Haddad, N. M. 1999. Corridor and distance effects on interpatch movements – a landscape experiment with butterflies. *Ecological Applications* 9(2): 612-22.

Haggett, P. 1963. Scale components in geographical problems. In *Frontiers in Geographical Teaching*, eds. Chorley, R. J., and Haggett, P., pp.164-185. London, U.K.: Methuen and Company Limited.

Haines-Young, R., Green, D. R., and Cousins, S. H., eds. 1993. *Landscape Ecology and GIS*. Bristol: Taylor and Francis, Inc.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396(6706): 41-9.

———. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87(2): 209-19.

Hanski, I. A. and Gilpin, M. E., eds. 1997. Metapopulation Biology. New York, NY: Academic Press.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* 42 (1-1): 89-103.

Harary, F. 1969. *Graph Theory*. Reading, MA: Addison-Wesley.

Hargis, C. D., Bissonette, J. A., and David, J. L. 1997. Understanding measures of landscape pattern. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J.A., Chapter 9. New York: Springer-Verlag.

Hargrove, W. W. and Pickering, J. 1992. Pseudoreplication – a sine quo non for regional ecology. *Landscape Ecology* 6(4): 251-8.

Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* 9(4): 845-54.

Hepinstall, J. A. and Harrison, D. J. 2004. Utility of forest carnivores (American marten and Canada lynx) as umbrella species for biodiversity conservation. In *Conference proceedings of Carnivores 2004 – Expanding Partnerships in Carnivore Conservation*, p.17. Sante Fe, NM: Defenders of Wildlife, 14-17 November.

Hobbs, R. J. 1992. Corridors for conservation – solution or bandwagon? *Trends in Ecology and Evolution* 7: 389-92.

———. 2002. Habitat networks and biological conservation. In *Applying landscape ecology in biological conservation*, ed. Gutzwiller, K. J., Chapter 9. New York, NY: Springer-Verlag.

Hobbs, R. J. and Wilson, A. M. 1998. Corridors – theory, practice and the achievement of conservation objectives. In *Key Concepts in Landscape Ecology*, eds. Dover, J.W., and Bunce, R. G. H., pp. 265-279. Preston, U.K.: International Association for Landscape Ecology.

Hodges, K. E. 2000a. The ecology of snowshoe hares in northern boreal forests. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S. and Squires, J. R., Chapter 6. Boulder, CO: University Press of Colorado.

———. 2000b. Ecology of snowshoe hares in southern boreal and montane forests. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S. and Squires, J. R., Chapter 7. Boulder, CO: University Press of Colorado.

Hooge, P. N. and Eichenlaub, B. 1997. Animal movement extension to Arcview ver. 1.1. Anchorage, AK: Alaska Science Center – Biological Science Office, U.S. Geological Survey.

Ingegnoli, V. 2002. *Landscape Ecology – A Widening Foundation.* New York: Springer-Verlag.

Jennrich, R. I. and Turner, F. B. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* 22: 227-37.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.

Karieva, P. M. 1990. Population dynamics in spatially complex environments – theory and data. *Philosophical Transactions of the Royal Society of London B* 330:175-90.

Keitt, T., Franklin, A., and Urban, D. 1995. Landscape analysis and metapopulation structure. In *Recovery plan for the Mexican spotted owl*, Volume II, Chapter 3. Albuquerque, NM: USDI Fish and Wildlife Service.

Keitt, T. H., Urban, D. L., and Milne, B. T. 1997. Detecting Critical Scales in Fragmented Landscapes. *Conservation Ecology* [online] 1(1) <http://www.ecologyandsociety.org/vol1/iss1/art4/manuscript.frames.html> (Accessed 29 August 2004).

Kie, J. G., Baldwin, J. A., and Evans, C. J. 1996. CALHOME – A program for estimating animal home ranges. *Wildlife Society Bulletin*, 24 (2): 342-4.

King, A.W. 1997. Hierarchy Theory – A Guide to System Structure for Wildlife Biologists. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J.A., Chapter 7. New York: Springer-Verlag.

Knick, S. T. and Dyer, D. L. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61(1): 75-85.

Knight, R. L. and Landres, P. B. 2002. Central concepts and issues of biological conservation. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 2. New York, NY: Springer-Verlag.

Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68: 845-51.

———. 1991. Snowshoe hare, Lepus americanus, use of forest successional stage and population changes during 1985-1989 in north-central Washington. *Canadian Field Naturalist*, 105: 291-3.

Koehler, G. M., Hornocker, M. G., and Hash, H. S. 1979. Lynx movements and habitat use in Montana. *Canadian Field-Naturalist* (4): 441-2.

Koehler, G. M. and Brittell, J. D. 1990. Managing spruce-fir and habitat for lynx and snowshoe hares. *Journal of Forestry* 88: 10-14.

Koehler, G. M. and Aubry, K. B. 1994. Lynx. In *The scientific basis for conserving forest carnivores – American marten, fisher, lynx and wolverine in the western United States*, eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Lyon, L. J., and Zielinski, W. J., pp. 74-98. RMRS-GTR RM-254. Fort Collins, CO: USDA Forest Service.

Koestler, A. 1969. Beyond atomism and holism – the concept of the holon. In *Beyond reductionism*, eds. Koestler, A. and Smythies, J. R., pp. 192-232. London, U.K.: Hutchinson.

Kotlier, N. B., and Wiens, J. A. 1990. Multiple scales of patchiness and patch structure – a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-60.

Krebs, C. J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K. E., and Boutin, S. 2001. Estimating snowshoe hare population density from pellet plots – a further evaluation. *Canadian Journal of Zoology* 79: 1-4.

Lambeck, R. J. 1997. Focal species – a multi-species umbrella for nature conservation. *Conservation Biology* 11: 849-56.

Leopold, A. 1949. *A Sand County Almanac*. New York: Oxford University Press.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-83.

Lillybridge, T. R., Kovalchik, B. L., Williams, C. K., and Smith, B. G. 1995. *Field guide for forested plant associations of the Wenatchee National Forest*. General Technical Report PNW-GTR-359. Pacific Northwest Research Station, USDA Forest Service.

Litvaitis, J. A. 1992. Niche relations between coyotes and sympatric Carnivora. In *Ecology and management of the eastern coyote,* ed. Boer, A. H., pp. 73-85. Fredericton, NB: University of New Brunswick Wildlife Research Unit.

Litvaitis, J. A., Sherbourne, J. A., and Bissonette, J. A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. *Journal of Wildlife Management* 49: 866-73.

MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography, *Monographs in Population Biology*, no.1. Princeton, NJ: Princeton University press.

Mandelbrot, B. B. 1967. How long is the coast of Britain? – statistical self-similarity and fractional dimension. *Science* 156: 636-8.

Manly, B., McDonald, L., and Thomas, D. 1993. Resource selection by animals – statistical design and analysis for field studies. London, U.K.: Chapman and Hall.

McClean, S. A., Rumble, M. A., King, R. M., and Baker, W. L. 1997. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* 62(2): 793-801.

McIntyre, S. and Hobbs, R. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models: *Conservation Biology* 13: 1282-92.

McKelvey, K. S., Ortega, Y. K., Koehler, G. M., Aubry, K. B., and Brittell, J. D. 2000a. Theoretical insights into the population viability of lynx. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 2. Boulder, CO: University Press of Colorado.

McKelvey, K. S., Ortega, Y. K., and Aubry, K. B. 2000b. History and distribution of lynx in the contiguous United States. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 8. Boulder, CO: University Press of Colorado.

McKelvey, K. S., Ortega, Y. K., Koehler, G. M., Aubry, K. B., Brittell, J. D. 2000c. Canada lynx habitat and topographic use patterns in North Central Washington – a reanalysis. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 10. Boulder, CO: University Press of Colorado.

McNab, W. H. and Avers, P. E. 1994. *Ecological Subregions of the United States*. Variable pagination. Section Descriptions, WO-WSA-5. Washington, DC: USDA Forest Service.

Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. *Journal of Mammalogy* 58: 676-7.

———. 1983. *A Handbook of Animal radio-tracking*. Minneapolis, MN: University of Minnesota Press.

Mills, L. S., Pilgrim, K. L., Schwartz, M. K., and McKelvey, K. S. 2000. Identifying lynx and other North American felids based on mtDNA analysis. *Conservation Genetics* 1: 285-8.

Milne, B. T., Johnson, K. M., and Forman, R. T. T. 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. *Landscape Ecology* 2: 101-10.

Mladenoff, D. J., Sickley, T. A., Haight, R. G., and Wydeven, A. P. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9(2): 279-94.

Mladenoff, D. J. and Sickley, T. A. 1998. Assessing potential gray wolf restoration in the northeastern United States – A spatial prediction of favorable habitat and potential population levels. *Journal of Wildlife Management* 62(1): 1-10.

Morrison, M. L., Marcot, B. G., and Mannan, R. W. 1992. *Wildlife-Habitat Relationships – Concepts and Applications*. Madison, WI: University of Wisconsin Press.

Mowat, G., Poole, K. G., and O'Donoghue, M. 2000. Ecology of lynx in northern Canada and Alaska. In *Ecology and Conservation of Lynx in the United States,* tech eds. L. F. Ruggiero, Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 9. Boulder, CO: University Press of Colorado.

Murray, D. K. and Boutin, S. 1991. The influence of snow on lynx and coyote movements – Does morphology affect behavior? *Oecologia* 88: 463-9.

Murray, D. L., Boutin, S., and O'Donoghue, M., 1994, Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology* 72: 1444-51.

Neu, C. W., Byers, C. R., and Peek, J. M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 42: 172-4.

Noon, B. R. and Dale, V. H. 2002. Broad-scale ecological science and its application. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 3. New York, NY: Springer-Verlag.

Noss, R. F. 1987. Corridors in real landscapes – a reply to Simberloff and Cox.*Conservation Biology* 1: 159-64.

———. 1991. Landscape connectivity – different functions at different scales. In *Landscape Linkages and Biodiversity*, ed. Hudson, W. E., pp. 27-39. Washington, DC: Island Press.

———. 1992. The Wildlands Project Land Conservation Strategy: *Wild Earth*, Special Issue no.1: 10-25.

Noss, R. F. and Cooperrider, A. Y. 1994. *Saving Nature's Legacy – Protecting and Restoring Biodiversity*. Washington, DC: Island Press.

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T., and Paquet, P. C. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10: 949-63.

Noss, R. F., O'Connell, M. A., and Murphy, D. D. 1997. *The Science of Conservation Planning*. Washington, DC: Island Press.

O'Donoghue, M., Boutin, S., Krebs, C. J., and Hofer, E. J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* v.74: 115-21.

Odum, E. P. and Kuenzler, E. J. 1955. Measurement of territory and home range size in birds. *Auk* 72: 128-37.

Oellermann, O. R. 1996. Connectivity and edge-connectivity in graphs – a survey. *Congr. Numer.* 116: 66-95.

O'Neill, R. V., Milne, B. T., Turner, M. G., and Gardner, R. H. 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* 2: 63-9.

Opdam, P. 1990. Dispersal in fragmented populations – the key to survival. In *Species Dispersal in Agricultural Habitats*, eds. Bunce, R.G.H., and Howard, D. C., pp. 3-17. London, U.K.: Belhaven Press.

———. 2002. Assessing the conservation potential of habitat networks. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 21. New York, NY: Springer-Verlag.

Orians, G. H. and Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. *American Naturalist*, Supplement S, 137: 29-49.

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., and Revilla, E. 2000. Iberian lynx in a fragmented landscape – predispersal, dispersal, and postdispersal habitats. *Conservation Biology* 14(3): 809-18.

Pearson, S. M., Turner, M. G., Gardner, R. H., O'Neill, R. V. 1996. An organism based perspective of habitat fragmentation. In *Biodiversity in Managed Landscapes – Theory and Practice,* ed. Szaro, R.C., pp.77-95. Oxford, U.K.: Oxford University Press.

Periera, J. M. and Itami, R. M. 1991. GIS-based habitat modeling using logistic multiple regression – a study of the Mt. Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57: 1475-86.

Pickett, S. T. A., Parker, V. T., and Fiedler, P. 1992. The new paradigm in ecology – Implications for conservation biology above the species level. In *Conservation Biology – The Theory and Practice of Nature Conservation, Preservation, and Management,* eds. Fiedler, P., Jain, S. K., pp. 65-8. New York: Chapman and Hall.

Pickett, S. T. A. and Cadenasso, M. L. 1995. Landscape Ecology – Spatial heterogeneity in ecological systems. *Science* 269: 331-4.

Pickett, S. T. A. and Ostfeld, R. S. 1995. The shifting paradigm in ecology. In *A New Century for Natural Resources Management,* eds. Knight, R. L. and Bates, S. K., pp. 261-79. Washington, DC: Island Press.

Pickett, S. T. A. and Rogers, K. H. 1997. Patch dynamics – the transformation of landscape structure and function. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J.A., Chapter 4. New York: Springer-Verlag.

Plotnik, R. E., Gardner, R. H., and O'Neill, R. V. 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology* 8: 201-11.

Poole, K. G. 1997a. Characteristics of an unharvested lynx population during snowshoe hare decline. *Journal ofWildlife Management* 58(4): 608-18.

———. 1997b. Dispersal patterns of lynx in the Northwest Territories. *Journal of Wildlife Management* 61(2): 497-505.

Poole, K. G., Wakelyn, L. A., and Nicklen, P. N. 1996. Habitat selection by lynx in the Northwest Territories. *Canadian Journal of Zoology* 74: 845-50.

Quinn, N. W. S., and Parker, G. 1987. Lynx. In *Wild furbearer management and conservation in North America,* eds. Novak, N., Baker, J., and Obbard, M., pp. 682-95. Toronto, Ontario: Ministry of Natural Resources.

Ricketts, T. H. 2001. The matrix matters – effective isolation in fragmented landscapes. *American Naturalist* 158(1): 87-99.

Risser, P. G. 1999. Landscape ecology – Does the science only need to change at the margin? In *Landscape Ecological Analysis – Issues and Applications,* eds. Klopatek, J. M. and Gardner, R. H., Chapter 1. New York: Springer-Verlag.

Risser, P. G., Karr, J. R., and Forman, R. T. T. 1984. *Landscape ecology – Direction and approaches.* Special Publication no.3. Champaign, IL: Illinois Natural History Survey.

Ritchie, M.E. 1997. Populations in a landscape context – sources, sinks, and metapopulations. In *Wildlife and Landscape Ecology – Effects of Pattern and Scale,* ed. Bissonette, J.A., pp.160-84. New York: Springer-Verlag.

Rosenberg, D. K., Noon, B. R., Megahan, J. W., and Meslow, E. C. 1998. Compensatory behavior of Ensatina eschscholtzii in biological corridors – a field experiment. *Canadian Journal of Zoology* 76(1): 117-33.

Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Lyon, L. J., and Zielinski, W. J., tech. eds. 1994. *The scientific basis for conserving forest carnivores – American marten, fisher, lynx, and wolverine in the western United States*. RMRS-GTR RM-254. Fort Collins, CO: USDA Forest Service.

Ruggiero, L. F. and McKelvey, K. S. 2000. Toward a defensible lynx conservation strategy – a framework for planning in the face of uncertainty. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 1. Boulder, CO: University Press of Colorado.

Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., tech. eds. 2000a. *Ecology and conservation of lynx in the United States*. Boulder, CO: University Press of Colorado.

Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R. 2000b. The scientific basis of lynx conservation – qualified insights. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 16. Boulder, CO: University Press of Colorado.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77(4): 1210-25.

Schwartz, M. K., Mills, L. S., McKelvey, K. S., Ruggiero, L. F., and Allendorf, F. W. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* 415: 520-2.

Shenk, T. M., and Franklin, A. B., eds. 2001. *Modeling in Natural Resource Management – Development, Interpretation, and Application*. Washington, Covelo: London, Island Press.

Simberloff, D. S., Farr, J. A., Cox, J., and Mehlman, D. W. 1992. Movement corridors – conservation bargains or poor investments? *Conservation Biology* 6: 493-504.

Singleton, P. H. and Lehmkuhl, J. F. 2000. *I-90 Snoqualmie Pass Wildlife Habitat Linkage Assessment*. Wenatchee, WA: Pacific Northwest Research Station – Wenatchee Forestry Sciences Lab, USDA Forest Service.

Singleton, P. H., Gaines, W. L., and Lehmkuhl, J. F. 2002. Landscape permeability for large carnivores in Washington – a geographic information system weighted-distance and least-cost corridor assessment. Res. Pap. PNW-RP-549. Portland, OR: Pacific Northwest Research Station, USDA Forest Service.

Skiena, S. 1990. Implementing Discrete Mathematics: Combinatorics and Graph Theory with Mathematica. Redwood City, CA: Addison-Wesley.

Slough, B. G. 1996. Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management* 60(4): 946-61.

Squires, J. R. and Laurion, T. 2000. Lynx home range and movement in Montana and Wyoming – preliminary results. In *Ecology and Conservation of Lynx in the United States,* tech eds. Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R., Chapter 11. Boulder, CO: University Press of Colorado.

Stauffer, D. and Aharony, A. 1992. *Introduction to Percolation Theory*, 2nd ed. London: Taylor and Francis.

Stenseth, N. C., Falck, W., Chan, K., Bjørnstad, O. N., O'Donoghue, M., Tong, H., Boonstra, R., Boutin, S., Krebs, C. J., and Yoccoz, N. G. 1998. From patterns to processes – phase and density dependencies in the Canadian lynx cycle. *Proceedings of the National Academy of Sciences* 95: 15430-5.

Stoms, D. M., Davis, F. W., and Cogan, C. B. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. *Photogrammetric Engineering and Remote Sensing* 58: 843-50.

Soulé, M. E., ed. 1986. *Conservation Biology – Science of Diversity and Scarcity*. Sunderland, Sinauer Associates.

Soulé, M. E. and Terborgh, J. 1999a. Conserving nature at regional and continental scales – a scientific program for North America. *Bioscience* 49(10): 809-17.

Soulé, M. E. and Terborgh, J., eds. 1999b. *Continental Conservation — Scientific Foundations of Regional Reserve Networks*. Washington, D.C., Covelo, CA: The Wildlands Project/ Island Press.

Sutcliffe, O. L. and Thomas, C. D. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (Aphantopus hyperantus) between woodland clearings. *Conservation Biology* 10(5): 1359-65.

Taylor, P. D., Fahrig, L., Henein, K., and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68(3): 571-3.

Terborgh, J., Estes, J. A., Paquet, P., Ralls, K., Boyd, D., Miller, B., and Noss, R. F. 1999. The role of top carnivores in regulating terrestrial ecosystems. *Wild Earth* 9(2): 42-56.

Tiebout, III, H. M. and Anderson, R. A. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. *Conservation Biology* 11(3): 620-7.

Troll, C. 1939. *Luftbildplan und ökologische Bodenforschung* ('Aerial photography and ecological studies of the earth'). Berlin: Zeitschrift der Gesellschaft für Erdkunde.

Turner, M. G., Gardner, R. H., and O'Neill, R. V. 2001. *Landscape Ecology in Theory and Practice – Pattern and Process*. New York, NY: Springer-Verlag.

Urban, D. and Keitt, T. 2001. Landscape connectivity – a graph-theoretic perspective. *Ecology* 82(5): 1205-18.

USFWS, 2001, Management of Canada lynx in the Cascades geographic areas of Oregon and Washington, A White Paper Prepared by the Offices of Region 1 of the U.S. Fish & Wildlife Service, Apr. 10, 2001.

von Bertalanffy L. 1973. *General System Theory,* (Revised Edition). New York: George Braziller.

Vos, C. C., Baveco, H., and Grashof-Bokdam, C. J. 2002. Corridors and species dispersal. In *Applying landscape ecology in biological conservation,* ed. Gutzwiller, K. J., Chapter 6. New York, NY: Springer-Verlag.

Walker, R. and Craighead, F. L. 1997. Analyzing wildlife movement corridors in Montana using GIS. *Proceedings of the 1997 ESRI User Conference*.

Ward, R. P. and Krebs, C. J. 1985. Behavioral responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology* 63: 2817-24.

Wennergren, U., Ruckelshaus, M., and Kareiva, P. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* 74(3): 349-56.

White, G. C. and Garrott, R. A. 1990. *Analysis of wildlife radio-tracking data*. San Diego, CA: Academic Press.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-97.

———. 1995. Landscape mosaics and ecological theory. In *Mosaic Landscapes and Ecological Processes,* eds. Hannson, L., Fahrig, L., and Merriam, G., pp.1-26. London: Chapman and Hall.

———. 1996. Wildlife in patchy environments – Metapopulations, mosaics, and management. In *Metapopulations and Wildlife Conservation*, ed. McCullough, D.R., pp. 53-85. Washington, DC: Island Press.

———. 1997. Metapopulation dynamics and landscape ecology. In *Metapopulation Biology – Ecology, Genetics, and Evolution,* eds. Hanski, I.A. and Gilpin, M.E., pp. 69-92. San Diego, CA: Academic Press.

———. 1999. The Science and practice of landscape ecology. In *Landscape Ecological Analysis – Issues and Applications*, eds. Klopatek, J. M. and Gardner, R. H., Chapter 16. New York: Springer-Verlag.

———. 2002. Central Concepts and Issues of Landscape Ecology. In *Applying Landscape Ecology in Biological Conservation*, ed. Gutzwiller, K.J., Chapter 1. New York: Springer-Verlag.

Wiens, J. A. and Milne, B. T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3: 87-96.

Wiens, J. A., Stenseth, N. C., van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369-80.

Williams, C. K., and Lillybridge, T. R. 1983. *Forested plant associations of the Okanogan National Forest*. Report R6-Ecol-132b-1983. Portland, OR: USDA Forest Service, Pacific Northwest Region.

Wildlands Project. 2002. http://www.twp.org/ (Accessed 19 November 2004).

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9: 25-36.

———. 1997a. The application of neutral landscape models in conservation biology. *Conservation Biology* 11(5): 1069-80.

———. 1997b. The Theory of conservation biology. *Conservation Biology* 11: 1436-40.

———. 1999. Is landscape connectivity necessary and sufficient for wildlife management? In *Forest Fragmentation – Wildlife and Management Implications*, eds. Rochelle, J. A., Lehmann, L. A., and Wisniewski, J., pp. 97-115. Leiden, Boston, Köln, Brill.

———. 2002. Using percolation theory to assess landscape connectivity an effects of habitat fragmentation. In *Applying Landscape Ecology in Biological Conservation*, ed. Gutzwiller, K.J., Chapter 7. New York, Springer-Verlag.

With, K. A., and Crist, T. O. 1995. Critical thresholds in species responses to landscape structure. *Landscape Ecology* 9: 25-36.

With, K. A., and King, A. W. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79: 319-29.

With, K. A., Gardner, R. H., and Turner, M. G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78: 151-69.

Withers, M. A., and Meentemeyer, V. 1999. Concepts of scale in landscape ecology. In *Landscape Ecological Analysis – Issues and Applications*, eds. Klopatek, J. M. and Gardner, R. H., pp.205-52. New York: Springer-Verlag.

Wolfe, M. L., Debyle, N.V., Winchell, C. S., and McCabe, T.R. 1982. Snowshoe hare cover relationships in northern Utah. *Journal of Wildlife Management* 46: 662-70.

Wolff, J.O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* 50(1): 111-30.

Wolfram Research, Inc., Mathematica, Version 4.1, Champaign, IL (2001).

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164-8.

Weaver, J. L., Paquet, P.C., and Ruggiero, L. F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10(4): 964-76.

Wu, J. and Hobbs, R. 2002. Key issues and research priorities in landscape ecology – an idiosyncratic synthesis. *Landscape Ecolog*y 17: 355-65.

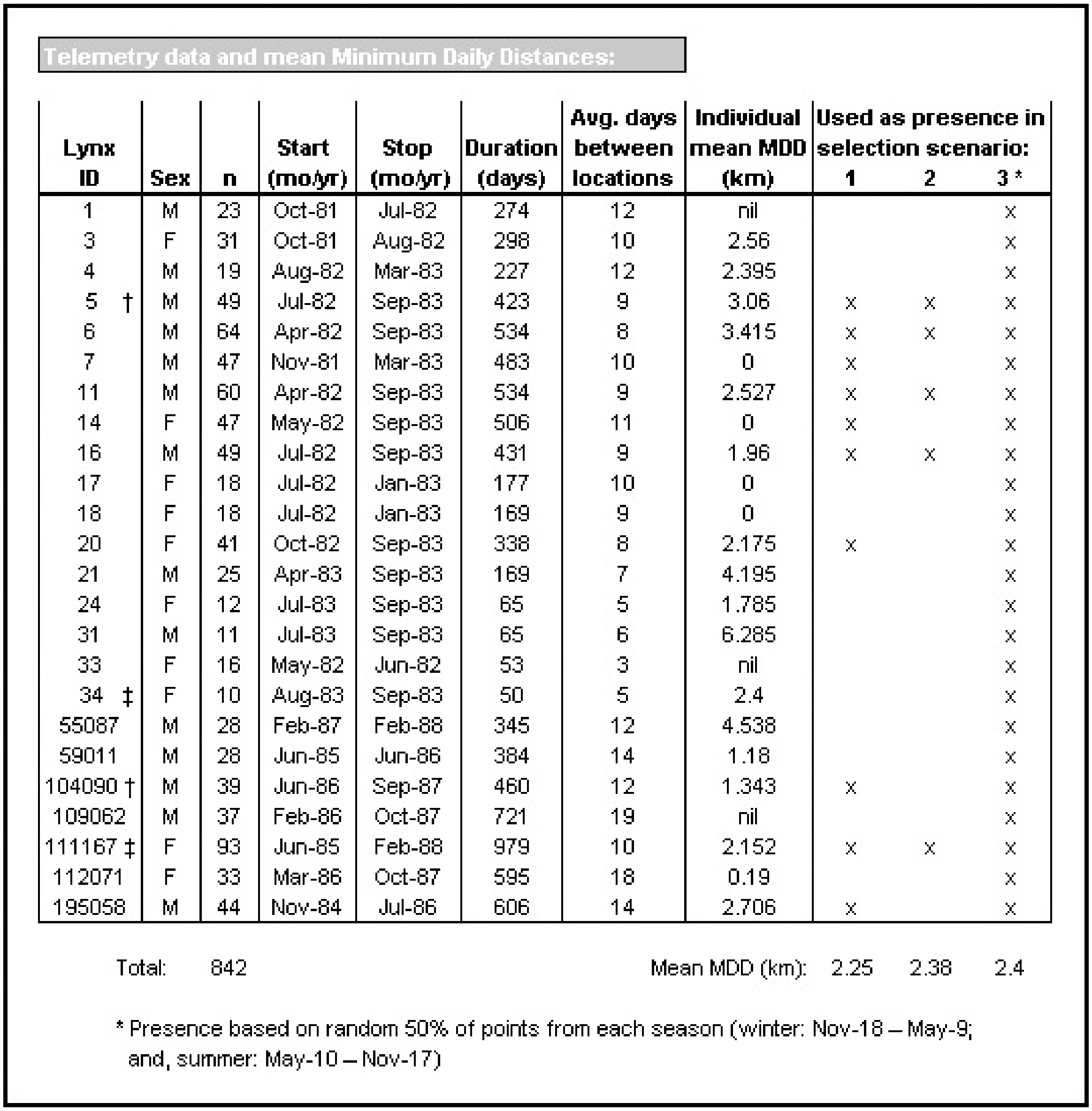
Yahner, R. H. and Mahan, C. G. 2002. Animal behavior in fragmented landscapes. In *Applying Landscape Ecology in Biological Conservation*, ed. Gutzwiller, K. J., Chapter 15. New York: Springer-Verlag.

Yellowstone to Yukon Conservation Initiative. 1997. http://www.twp.org/ (Accessed 19 November 2004).

APPENDICES

APPENDIX A

TELEMETRY DATA
AND MEAN MINIMUM DAILY DISTANCES



Telemetry data and mean Minimum Daily Distances:

Lynx ID	Sex	n	Start (mo/yr)	Stop (mo/yr)	Duration (days)	Avg. days between locations	Individual mean MDD (km)	Used as presence in selection scenario: 1	2	3 *
1	M	23	Oct-81	Jul-82	274	12	nil			x
3	F	31	Oct-81	Aug-82	298	10	2.56			x
4	M	19	Aug-82	Mar-83	227	12	2.395			x
5 †	M	49	Jul-82	Sep-83	423	9	3.06	x	x	x
6	M	64	Apr-82	Sep-83	534	8	3.415	x	x	x
7	M	47	Nov-81	Mar-83	483	10	0	x		x
11	M	60	Apr-82	Sep-83	534	9	2.527	x	x	x
14	F	47	May-82	Sep-83	506	11	0	x		x
16	M	49	Jul-82	Sep-83	431	9	1.96	x	x	x
17	F	18	Jul-82	Jan-83	177	10	0			x
18	F	18	Jul-82	Jan-83	169	9	0			x
20	F	41	Oct-82	Sep-83	338	8	2.175	x		x
21	M	25	Apr-83	Sep-83	169	7	4.195			x
24	F	12	Jul-83	Sep-83	65	5	1.785			x
31	M	11	Jul-83	Sep-83	65	6	6.285			x
33	F	16	May-82	Jun-82	53	3	nil			x
34 ‡	F	10	Aug-83	Sep-83	50	5	2.4			x
55087	M	28	Feb-87	Feb-88	345	12	4.538			x
59011	M	28	Jun-85	Jun-86	384	14	1.18			x
104090 †	M	39	Jun-86	Sep-87	460	12	1.343	x		x
109062	M	37	Feb-86	Oct-87	721	19	nil			x
111167 ‡	F	93	Jun-85	Feb-88	979	10	2.152	x	x	x
112071	F	33	Mar-86	Oct-87	595	18	0.19			x
195058	M	44	Nov-84	Jul-86	606	14	2.706	x		x
Total:		842					Mean MDD (km):	2.25	2.38	2.4

* Presence based on random 50% of points from each season (winter: Nov-18 – May-9; and, summer: May-10 – Nov-17)

APPENDIX B

PREDICTOR DATASET RECLASSIFICATIONS

Topographic classifications

Predictor datasets	Class Interval	#	Summary description
Elevation	100m	12	<1150m,1150-1250m,... ,2050-2150m,>2150m
"	150m	10	<950m,950-1100m,... ,2000-2150m,>2150m
"	200m	7	<1150m,1150-1350m,... ,1950-2150m,>2150m
Slope	10°	9	0°-10°;... ; 80°-90°
"	15°	6	0°-15°;... ; 75°-90°
"	30°	3	0°-30°;... ; 60°-90°
Aspect	45°	5	SW or Flat; W or S; NW or SE; N or E; NE
"	90°	3	SW or Flat; NW or SE; NE
"	180°	2	SW or Flat; NE

Landcover classifications:
Canopy Coverage

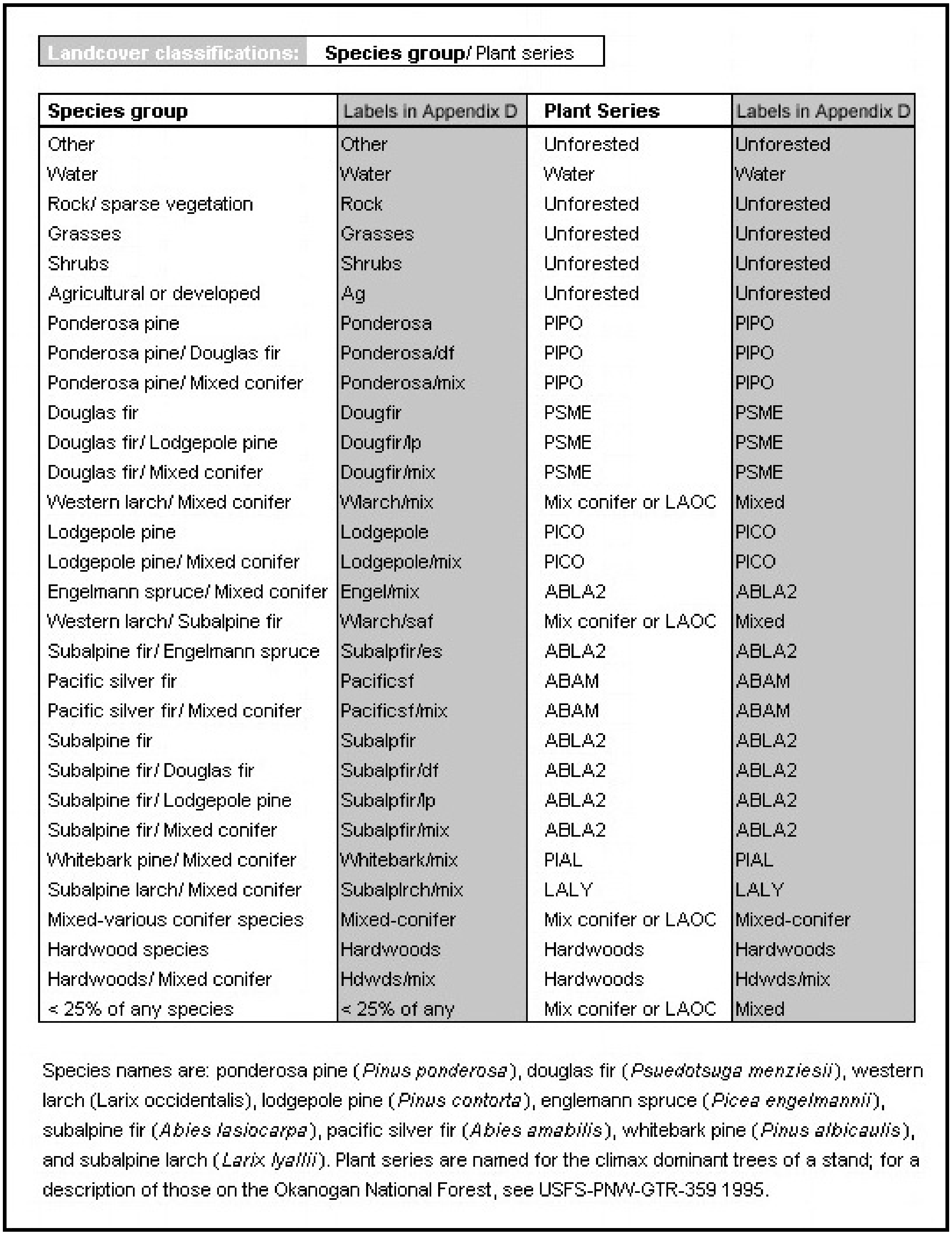
Original dataset	**Reclassed dataset**
71-100%	71-100%
51-70%	31-70%
31-50%	31-70%
11-30%	1-30%
1-10%	1-30%
Unforested	Unforested
Water	Water

Landcover classifications: **Stand structure**

Original dataset	Labels in Appendix D	**Reclassed dataset**	Labels in Appendix D
Water	Water	Water	Water
Rock	Rock	Unforested	Unforested
Grasses	Grass	Unforested	Unforested
Shrubs	Shrub	Unforested	Unforested
Agricultural or developed	Ag	Unforested	Unforested
Seed-Sap-Pole/SS	Seed-pole	Seed-Sap-Pole	Seed
Pole/SS	Pole	Poles without seed or sap	Pole
Pole-Small/SS	Pole-sm.	Poles without seed or sap	Pole
Pole/MSLD	Pole/MSLD	Poles without seed or sap	Pole
Pole/MS+	Pole/MS+	Poles without seed or sap	Pole
Small/SS	Small	Small without poles	Small
Small-Medium/SS	Small-md	Small without poles	Small
Small/MSLD	Small/MSLD	Small without poles	Small
Small/MS-	Small/MS-	Small without poles	Small
Small/MS++	Small/MS++	Small without poles	Small
Medium/SS	Medium	Medium without small	Medium
Medium-Large/SS	Medium-lg	Medium without small	Medium
Medium/MSLD	Medium/MSLD	Medium without small	Medium
Medium/MS+	Medium/MS+	Medium without small	Medium

Term	Description
Seed	<1" (and >1' high)
Sap	1" – 4.9"
Pole	5 – 8.9"
Small	10 – 20.9"
Medium	21 – 31.9"
Large	32 – 47.9"
SS	Single-size
MS	Multi-size
LD	Low density (< 40% of total canopy cover)
MSLD	Multi-size and low density

Term	Description
-	More canopy cover exists in trees smaller than this size class than in those larger
+	More canopy cover exists in trees larger than this size class than in those smaller
++	Provides additional information about old growth as defined by Region 6 for production of regional old growth maps. Small/MS++ meets the old growth definition at all elevations, while Small/MS+ meets the old growth definition for the true fir zone. Pole/MS++ meets the old growth definition at only the true fir zone.



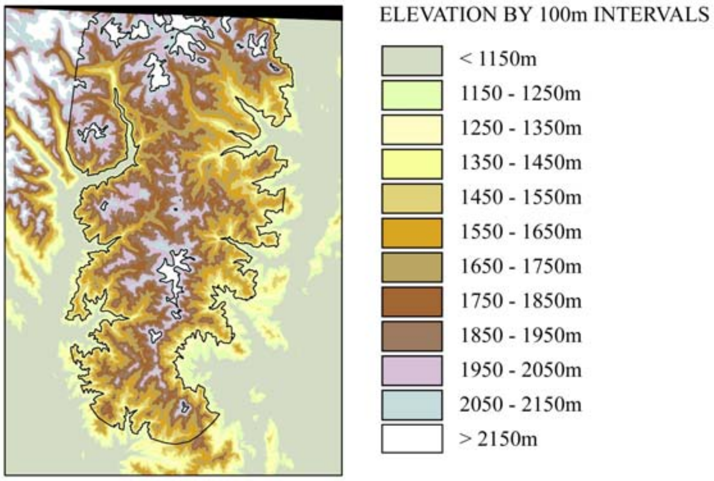
Landcover classifications: **Species group/** Plant series

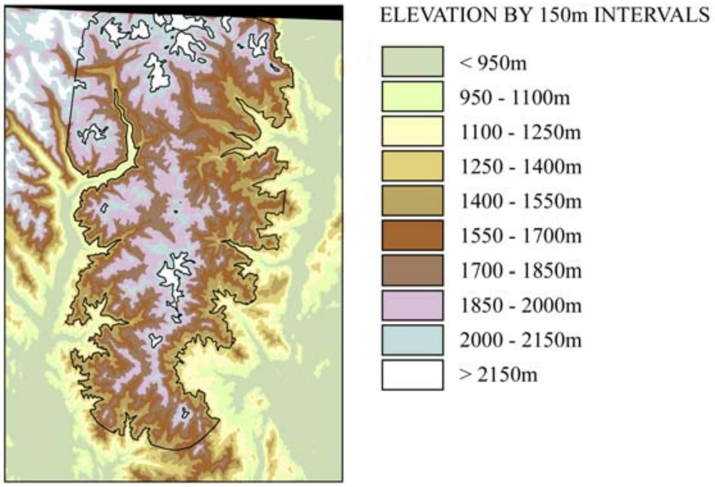
Species group	Labels in Appendix D	**Plant Series**	Labels in Appendix D
Other	Other	Unforested	Unforested
Water	Water	Water	Water
Rock/ sparse vegetation	Rock	Unforested	Unforested
Grasses	Grasses	Unforested	Unforested
Shrubs	Shrubs	Unforested	Unforested
Agricultural or developed	Ag	Unforested	Unforested
Ponderosa pine	Ponderosa	PIPO	PIPO
Ponderosa pine/ Douglas fir	Ponderosa/df	PIPO	PIPO
Ponderosa pine/ Mixed conifer	Ponderosa/mix	PIPO	PIPO
Douglas fir	Dougfir	PSME	PSME
Douglas fir/ Lodgepole pine	Dougfir/lp	PSME	PSME
Douglas fir/ Mixed conifer	Dougfir/mix	PSME	PSME
Western larch/ Mixed conifer	Wlarch/mix	Mix conifer or LAOC	Mixed
Lodgepole pine	Lodgepole	PICO	PICO
Lodgepole pine/ Mixed conifer	Lodgepole/mix	PICO	PICO
Engelmann spruce/ Mixed conifer	Engel/mix	ABLA2	ABLA2
Western larch/ Subalpine fir	Wlarch/saf	Mix conifer or LAOC	Mixed
Subalpine fir/ Engelmann spruce	Subalpfir/es	ABLA2	ABLA2
Pacific silver fir	Pacificsf	ABAM	ABAM
Pacific silver fir/ Mixed conifer	Pacificsf/mix	ABAM	ABAM
Subalpine fir	Subalpfir	ABLA2	ABLA2
Subalpine fir/ Douglas fir	Subalpfir/df	ABLA2	ABLA2
Subalpine fir/ Lodgepole pine	Subalpfir/lp	ABLA2	ABLA2
Subalpine fir/ Mixed conifer	Subalpfir/mix	ABLA2	ABLA2
Whitebark pine/ Mixed conifer	Whitebark/mix	PIAL	PIAL
Subalpine larch/ Mixed conifer	Subalplrch/mix	LALY	LALY
Mixed-various conifer species	Mixed-conifer	Mix conifer or LAOC	Mixed-conifer
Hardwood species	Hardwoods	Hardwoods	Hardwoods
Hardwoods/ Mixed conifer	Hdwds/mix	Hardwoods	Hdwds/mix
< 25% of any species	< 25% of any	Mix conifer or LAOC	Mixed

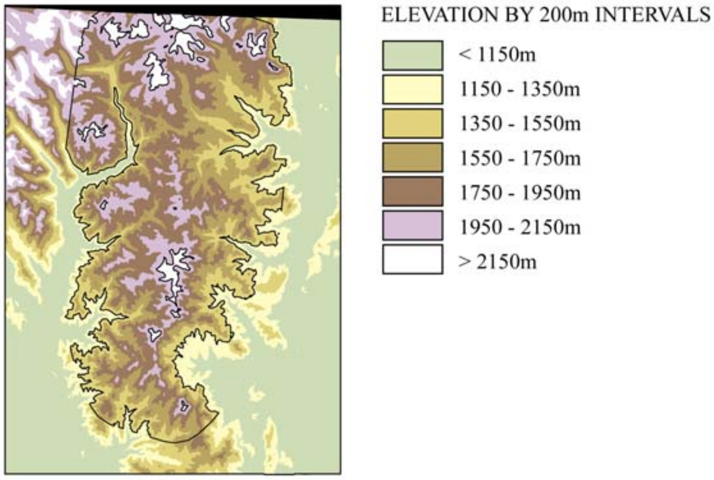
Species names are: ponderosa pine (*Pinus ponderosa*), douglas fir (*Psuedotsuga menziesii*), western larch (Larix occidentalis), lodgepole pine (*Pinus contorta*), englemann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), pacific silver fir (*Abies amabilis*), whitebark pine (*Pinus albicaulis*), and subalpine larch (*Larix lyallii*). Plant series are named for the climax dominant trees of a stand; for a description of those on the Okanogan National Forest, see USFS-PNW-GTR-359 1995.

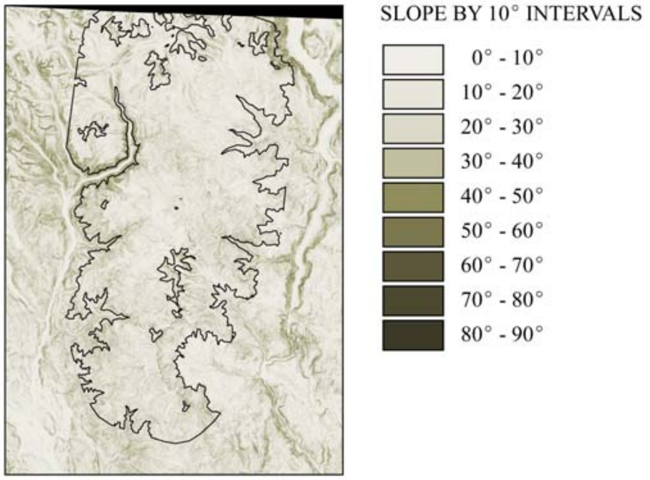
APPENDIX C

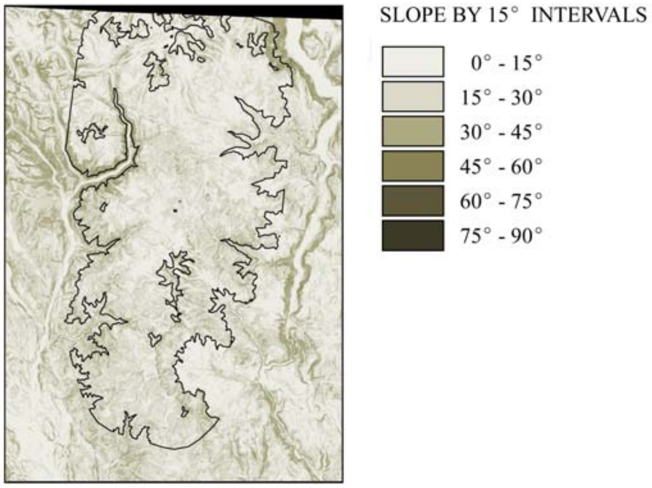
CANDIDATE PREDICTOR DATASETS

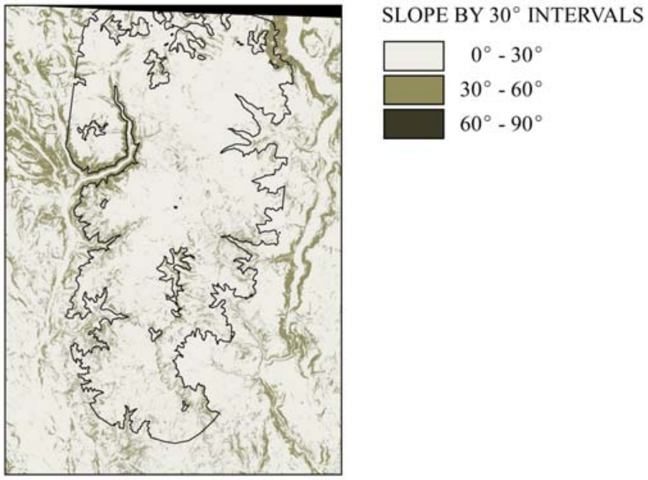

ELEVATION BY 100m INTERVALS
< 1150m
1150 - 1250m
1250 - 1350m
1350 - 1450m
1450 - 1550m
1550 - 1650m
1650 - 1750m
1750 - 1850m
1850 - 1950m
1950 - 2050m
2050 - 2150m
> 2150m

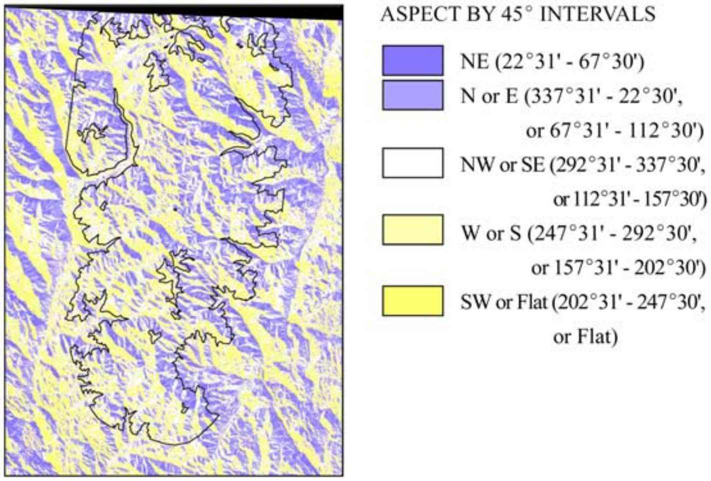

ELEVATION BY 150m INTERVALS
< 950m
950 - 1100m
1100 - 1250m
1250 - 1400m
1400 - 1550m
1550 - 1700m
1700 - 1850m
1850 - 2000m
2000 - 2150m
> 2150m

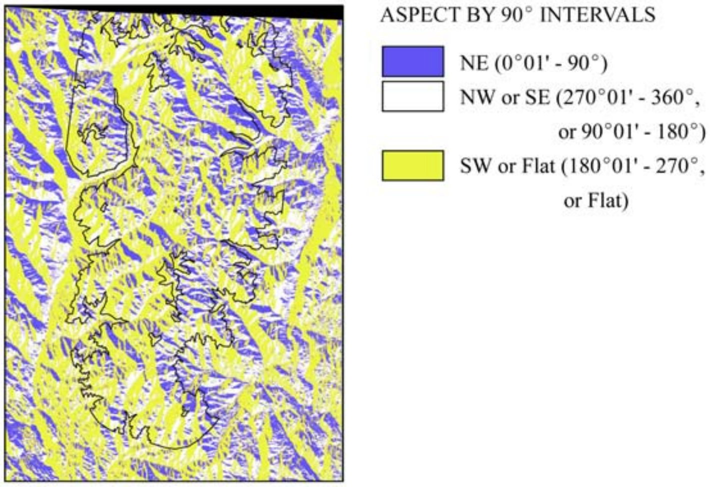

ELEVATION BY 200m INTERVALS
< 1150m
1150 - 1350m
1350 - 1550m
1550 - 1750m
1750 - 1950m
1950 - 2150m
> 2150m

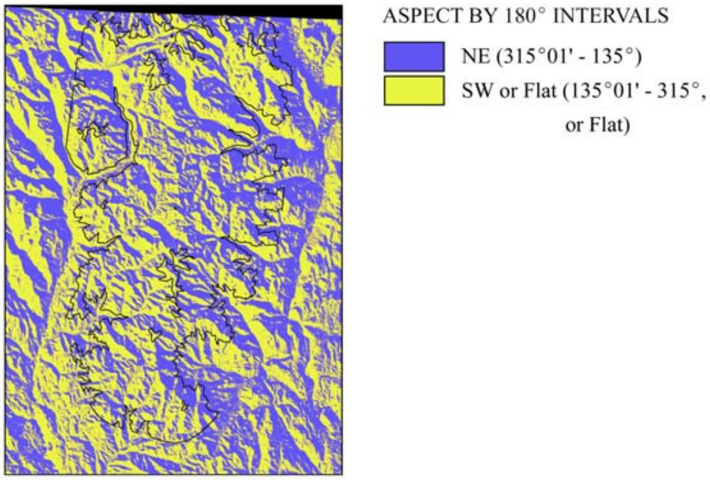

SLOPE BY 10° INTERVALS
0° - 10°
10° - 20°
20° - 30°
30° - 40°
40° - 50°
50° - 60°
60° - 70°
70° - 80°
80° - 90°

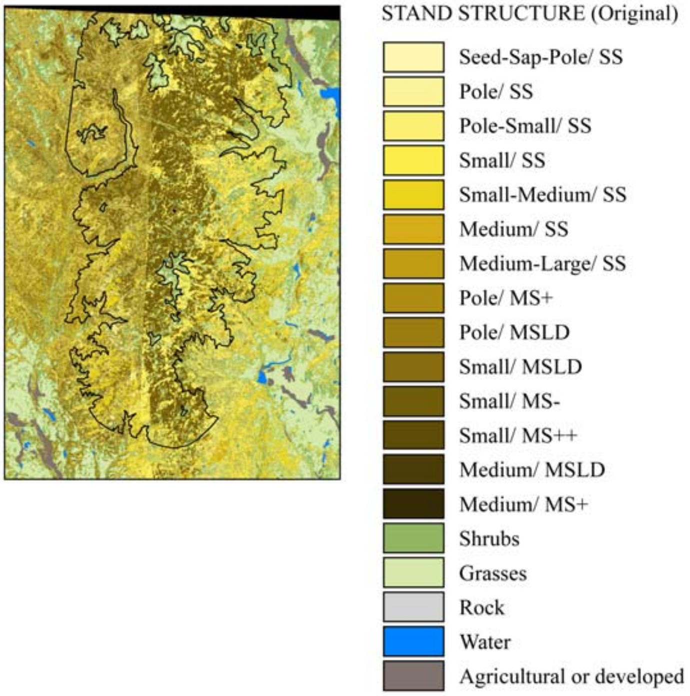

SLOPE BY 15° INTERVALS
0° - 15°
15° - 30°
30° - 45°
45° - 60°
60° - 75°
75° - 90°

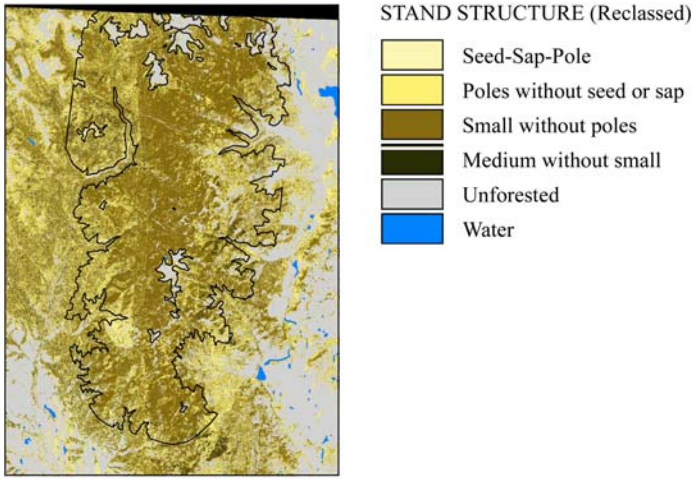

SLOPE BY 30° INTERVALS
0° - 30°
30° - 60°
60° - 90°

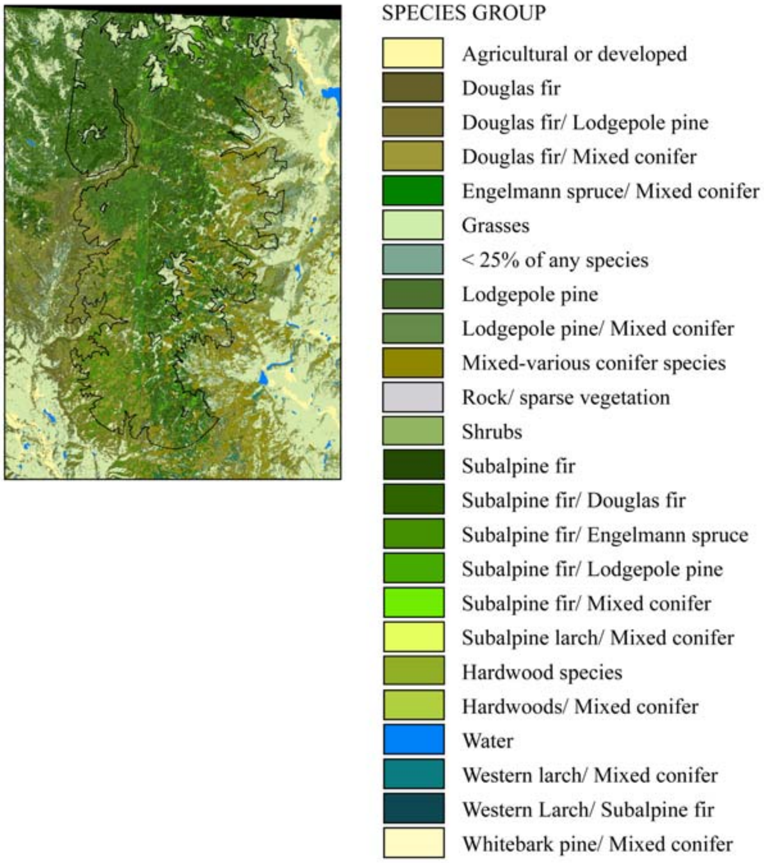

ASPECT BY 45° INTERVALS

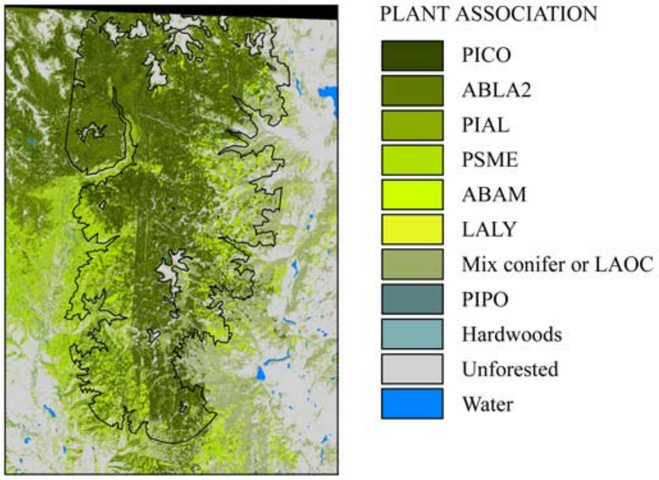

ASPECT BY 90° INTERVALS

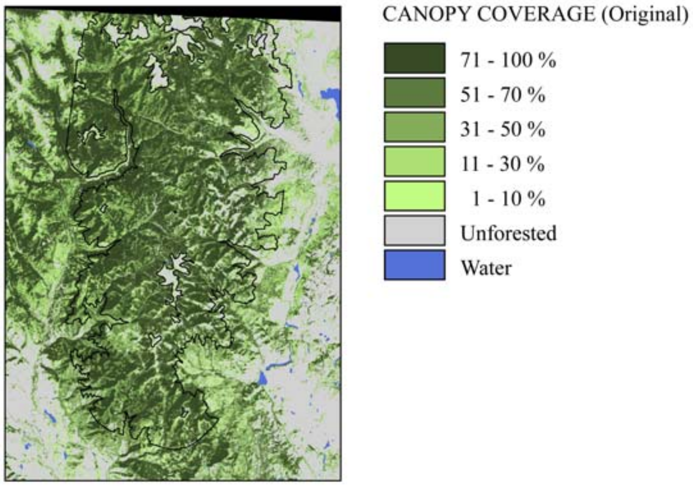

ASPECT BY 180° INTERVALS

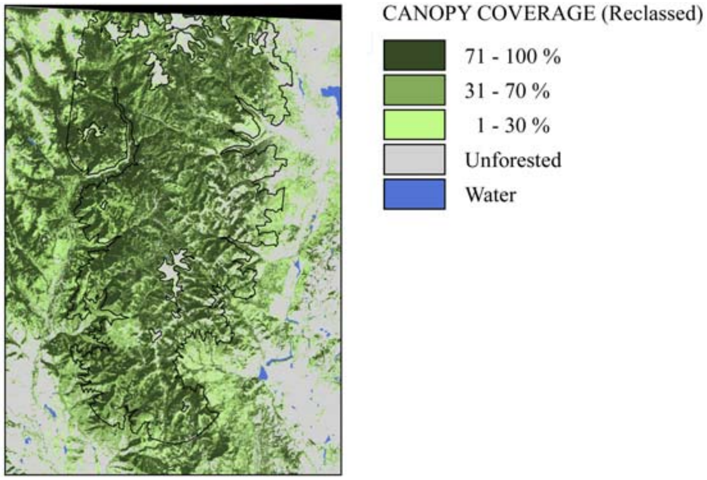

STAND STRUCTURE (Original)
Seed-Sap-Pole/ SS
Pole/ SS
Pole-Small/ SS
Small/ SS
Small-Medium/ SS
Medium/ SS
Medium-Large/ SS
Pole/ MS+
Pole/ MSLD
Small/ MSLD
Small/ MS-
Small/ MS++
Medium/ MSLD
Medium/ MS+
Shrubs
Grasses
Rock
Water
Agricultural or developed


STAND STRUCTURE (Reclassed)
Seed-Sap-Pole
Poles without seed or sap
Small without poles
Medium without small
Unforested
Water


SPECIES GROUP
Agricultural or developed
Douglas fir
Douglas fir/ Lodgepole pine
Douglas fir/ Mixed conifer
Engelmann spruce/ Mixed conifer
Grasses
< 25% of any species
Lodgepole pine
Lodgepole pine/ Mixed conifer
Mixed-various conifer species
Rock/ sparse vegetation
Shrubs
Subalpine fir
Subalpine fir/ Douglas fir
Subalpine fir/ Engelmann spruce
Subalpine fir/ Lodgepole pine
Subalpine fir/ Mixed conifer
Subalpine larch/ Mixed conifer
Hardwood species
Hardwoods/ Mixed conifer
Water
Western larch/ Mixed conifer
Western Larch/ Subalpine fir
Whitebark pine/ Mixed conifer


PLANT ASSOCIATION
PICO
ABLA2
PIAL
PSME
ABAM
LALY
Mix conifer or LAOC
PIPO
Hardwoods
Unforested
Water


CANOPY COVERAGE (Original)
71 - 100 %
51 - 70 %
31 - 50 %
11 - 30 %
1 - 10 %
Unforested
Water


CANOPY COVERAGE (Reclassed)
71 - 100 %
31 - 70 %
1 - 30 %
Unforested
Water

APPENDIX D

SELECTION OF BAYES MODEL INPUTS

lynxID 5	**JENNRICH-TURNER 90% Probability contour**
n = 49	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**χ2** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*nil*	*ns*		**1850-1950**	
" by 150m	*nil*	*ns*		1550-1700;**1850-2000**	
" by 200m	*nil*	*ns*		1350-1550;1550-1750;**1750-1950**	
SLOPE by 10°	*70–80 °*	*ns*		**0-10°**;20-30°	
" by 15°	*nil*	*ns*		**0-15°**	
" by 30°	*60–90 °*	*ns*		*nil*	
ASPECT by 45°	*nil*	*ns*		*nil*	
" by 90°	SW or Flat	*ns*		SW or Flat	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		**Small/MS-**	
" (reclassed)	*Water*	*ns*		Pole;**Small**	
SPECIES GROUP	*Other;* ***Water;*** *Wlarch/saf;Hardwoods/mix*	*ns*		**Mixed-conifer**	
plant association	***Water***;PIPO	*ns*		*nil*	
CANOPY (orig.)	***Water***	*ns*		*nil*	
" (reclassed)	***Water***	*ns*		*nil*	

** Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 6	**JENNRICH-TURNER 90% Probability contour**
M $n = 64$	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	13.558	7	1350-1450;1450-1550;**1750-1850;1850-1950;**2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*50-60 °*	*ns*		**10-20°**;20-30°;30-40°	
" by 15°	*60-75 °*	*ns*		**0-15°**;30-45°	
" by 30°	*60-90 °*	*ns*		**0-30°**;30-60°	
ASPECT by 45°	SW or Flat;**N or E**	*ns*		W or S;**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		**Small/MS-**	
" (reclassed)	*Water*	4.45	6	**Unforested**;Seed;Pole;**Small**;Medium	
SPECIES GROUP	*Subalplrch/mix;Water;Rock*	*ns*		*nil*	
plant association	*LALY*	*ns*		*nil*	
CANOPY (orig.)	*Water*	*ns*		31-50%	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *- Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 7	**JENNRICH-TURNER 90% Probability contour**
M n = 47	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1650-1750	*ns*		1650-1750;**1850-1950**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;**20-30°;30-40°**	
" by 15°	*60-70 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**N or E**	*ns*		**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Small/MS++;Small/MSLD;Small/MS+*	*ns*		**Small**;Small-md;**Small/MS-**	
" (reclassed)	*Water*	*ns*		Pole;**Small**	
SPECIES GROUP	*Ponderosa;Dougfir/lp;Subalpfir/df*	*ns*		Dougfir/mix;Subalpfir/es;**Mixed-conifer**	
plant association	*LALY*	20.248	10	**Mixed-conifer**;PSME;**PICO**	
CANOPY (orig.)	*Water*	*ns*		**Unforested**	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 11	**JENNRICH-TURNER 90% Probability contour**
M *n* = 60	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	**χ2** α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*nil*	45.549	7	1350-1450;...;1550-1650;**1650-1750;...;1850-1950**;2050-2150	
" by 150m	1250-1400	41.83	5	1400-1550;1550-1700;**1700-1850;1850-2000**;2000-2150	x
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;**20-30°**	
" by 15°	*60-75 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	*nil*	*ns*		*nil*	
" by 90°	**SW or Flat**	*ns*		**SW or Flat;**NW or SE	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	40.039	18	Pole-sm;Small-md;**Small/MS-**	
" (reclassed)	*Water*	19.544	6	Unforested;Seed;Pole;**Small**;Medium	
SPECIES GROUP	*Ponderosa;Wlarch/mix*	*ns*		Dougfir/mix;**Lodgepole;Subalpfir;**Mixed-conifer	
plant association	*LALY*;PIPO	29.157	10	Unforested;Mixed-conifer;PSME;**ABLA2;PICO**	x
CANOPY (orig.)	*Water*	*ns*		Unforested;**71-100%**	
" (reclassed)	*Water*	*ns*		Unforested;1-30%;**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 14	**JENNRICH-TURNER 90% Probability contour**
F *n* = 47	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	25.662	7	1350-1450;...;1550-1650;**1650-1750;...;1850-1950**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	23	8	**0-10°;10-20°**;20-30°;30-40°	
" by 15°	**0-15°**;*60-75 °*	23.899	5	**0-15°**;15-30°;30-45°	x
" by 30°	-	-		-	
ASPECT by 45°	NW or SE;**NE**	*ns*		NW or SE;**NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	43.728	18	Pole-sm;Small-md;**Small/MSLD;Small/MS-**	
" (reclassed)	*Water*	19.12	6	Unforested;Seed;Pole;**Small**;Medium	
SPECIES GROUP	Ponderosa;*Subalpfir/df*	*ns*		Dougfir/mix;**Lodgepole;Subalpfir**	x
plant association	*LALY*	35.723	10	Mixed-conifer;PSME;**ABLA2;PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested;**51-70%**	
" (reclassed)	*Water*	*ns*		Unforested	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 16	**JENNRICH-TURNER 90% Probability contour**
M n = 49	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	**χ2** α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	15.328	7	**1550-1650;1650-1750;**1950-2050;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*nil*	23.61	8	**0-10°;10-20°**;20-30°;30-40°	
" by 15°	**0-15°**	23.389	5	**0-15°**;15-30°;30-45°	x
" by 30°	-	-		-	
ASPECT by 45°	NW or SE;**NE**	*ns*		NW or SE;**NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD; Medium/MS+*	*ns*		Small-md;**Small/MS-**	
" (reclassed)	*Water*	*ns*		Pole;**Small**	
SPECIES GROUP	*Other;Water;Subalplrch/mix;* ***Hardwoods***	*ns*		**Lodgepole;Subalpfir**	
plant association	*Water;* ***Hardwoods*** *;LALY*	19.845	10	PSME;**PICO**	
CANOPY (orig.)	*Water*	*ns*		*nil*	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 20	**JENNRICH-TURNER 90% Probability contour**
F *n* = 41	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	*ns*		**1750-1850;1850-1950**;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;**20-30°**	
" by 15°	*60-75 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	SW or Flat;**N or E**	*ns*		*nil*	
" by 90°	SW or Flat	*ns*		SW or Flat;**NW or SE**	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Small/MS++;Medium/MSLD;Medium/MS+*	*ns*		**Small**;Small-md;**Small/MS-**	
" (reclassed)	*Water*;Medium	*ns*		Pole;**Small**	x
SPECIES GROUP	*Dougfir/lp;Subalpfir/df;Subalplrch/mix*	*ns*		Dougfir/mix;**Mixed-conifer**	
plant association	*Water;LALY*	*ns*		**Mixed-conifer;PICO**	
CANOPY (orig.)	*Water*	*ns*		*nil*	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 104090	**JENNRICH-TURNER 90% Probability contour**
M *n* = 39	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**χ2** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	**1850-1950**	*ns*		1450-1550;1550-1650;**1850-1950;1950-2050**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*70-80 °*	*ns*		**10-20°**	
" by 15°	*nil*	*ns*		**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	SW or Flat	*ns*		**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		Pole-sm;Small-md;**Small/MS-**	
" (reclassed)	*Water*	*ns*		Seed;**Small**	
SPECIES GROUP	Ponderosa;*Ponderosa/df;Subalplrch/mix*	*ns*		**Lodgepole**	x
plant association	*LALY*	*ns*		PSME;**PICO**	
CANOPY (orig.)	*Water*	*ns*		*nil*	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* χ*2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 111167	**JENNRICH-TURNER 90% Probability contour**
F *n* = 93	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	52.539	7	1350-1450;...;1550-1650;**1650-1750;...;1850-1950**;1950-2050;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;**20-30°**	
" by 15°	**0-15°**	*ns*		**0-15°**;15-30°;30-45°	x
" by 30°	-	-		-	
ASPECT by 45°	*nil*	*ns*		*nil*	
" by 90°	**SW or Flat**;NW or SE	*ns*		*nil*	
" by 180°	*nil*	*ns*		**SW or Flat**;NE	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	48.196	18	Grasses;Pole-sm;Small-md;**Small/MS-**	
" (reclassed)	*Water*	24.364	6	Unforested;Seed;Pole;**Small**;Medium	
SPECIES GROUP	*Ponderosa;Wlarch/mix*	*ns*		Grasses	
plant association	*LALY*;PIPO	34.043	10	Unforested;Mixed-conifer;PSME;**ABLA2;PICO**	x
CANOPY (orig.)	*Water*	*ns*		Unforested;**51-70%;71-100%**	
" (reclassed)	*Water*	*ns*		Unforested;1-30%;**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 195058	**JENNRICH-TURNER 90% Probability contour**
M *n* = 44	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	45.555	7	1350-1450;**1550-1650;...;1750-1850**;1850-1950;...;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*nil*	24.79	8	**0-10°;10-20°**;20-30°;30-40°	
" by 15°	**0-15°**	26.586	5	**0-15°**;15-30°;30-45°	x
" by 30°	-	-		-	
ASPECT by 45°	NW or SE;**NE**	9.262	4	NW or SE;**NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	38.808	18	Pole-sm;Small-md;**Small/MSLD;Small/MS-**	
" (reclassed)	Seed	15.878	6	Unforested;Seed;Pole;**Small**;Medium	x
SPECIES GROUP	*Ponderosa;Subalpfir/df;* ***Hardwoods***	*ns*		Dougfir/mix;**Lodgepole;Subalpfir**	
plant association	*LALY;* ***Hardwoods***	50.241	10	PSME;**PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested;**51-70%**	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 5	**JENNRICH-TURNER 90% Probability contour**
n = 49	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	**χ2** α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	19.8	7	1350-1450;1450-1550;**1550-1650;...;...;...;1950-2050**;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;10-20°;**20-30°;30-40°**	
" by 15°	*75-90 °*	*ns*		**0-15°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**NW or SE**	*ns*		**NW or SE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Water;Rock;Small/MS++*	*ns*		Small/MS-	
" (reclassed)	*Water*	*ns*		Pole; **Small**	
SPECIES GROUP	*Water;Rock;Subalp/rch/mix;Ponderosa/df;Ponderosa/*	*ns*		Subalpfir	
plant association	*Water;LALY*	*ns*		Subalpfir;**Mixed-conifer**	
CANOPY (orig.)	*Water*	*ns*		71-100%	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 6	**JENNRICH-TURNER 90% Probability contour**
M *n* = 64	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	**χ2** α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1450-1550	*ns*		1450-1550;**1850-1950;1950-2050**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	***40-50 °***;*50-60 °*	*ns*		0-10°	
" by 15°	*45-60 °*	*ns*		0-15°;**15-30°**;30-45°	
" by 30°	**30-60°**	*ns*		*nil*	
ASPECT by 45°	SW or Flat; **NE**	*ns*		*nil*	
" by 90°	NW or SE	*ns*		**SW or Flat;**NW or SE	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	***Small/MS***++	*ns*		Small/MS-	
" (reclassed)	Unforested	*ns*		**Small**	x
SPECIES GROUP	*Ponderosa;Subalpfir/df*	*ns*		*nil*	
plant association	*PIPO*	*ns*		**PICO**	
CANOPY (orig.)	Unforested	*ns*		Unforested;**71-100%**	x
" (reclassed)	-	-		-	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 7 M n = 47	**JENNRICH-TURNER 90% Probability contour** **FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	**1450-1550**;2050-2150	22.397	7	**1350-1450;1450-1550**;**1750-1850**;1850-1950;...;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		**20-30°**	
" by 15°	*60-75 °*	*ns*		*nil*	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	*nil*	9.72	4	W or S;NW or SE;**N or E;NE**	
" by 90°	SW or Flat	23.524	2	SW or Flat; **NW or SE; NE**	x
" by 180°	-	-			
STRUCTURE(orig.)	*Rock*	*ns*		*nil*	
" (reclassed)	Water	*ns*		Unforested; **Pole**	x
SPECIES GROUP	*Rock; Ponderosa/df*	*ns*		**Mixed-conifer**	
plant association	ABAM; ***Hardwoods***	*ns*		Unforested; **Mixed-conifer**	x
CANOPY (orig.)	Unforested	*ns*		Unforested	x
" (reclassed)	-	-		-	

** Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *– Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 11	**JENNRICH-TURNER 90% Probability contour**
M *n* = 60	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*1350-1450*;1450-1550	17.658	7	1550-1650;1650-1750;**1850-1950**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*50-60 °*	*ns*		*nil*	
" by 15°	*45-60 °*	*ns*		*nil*	
" by 30°	***30-60 °***	*ns*		*nil*	
ASPECT by 45°	SW or Flat;**NE**	*ns*		*nil*	
" by 90°	**NE**	*ns*		SW or Flat;**NE**	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		*nil*	
" (reclassed)	*Seed*	*ns*		**Small**	
SPECIES GROUP	*Ponderosa/df;Hardwoods*	*ns*		*nil*	
plant association	*Hardwoods;PIPO*	*ns*		*nil*	
CANOPY (orig.)	*nil*	*ns*		*nil*	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear* in normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 14 F *n* = 47	**JENNRICH-TURNER 90% Probability contour** **FINE-SCALE SELECTION (within Home Range)**				
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*1350-1450*	*ns*		**1550-1650**;1650-1750;**1750-1850**	
" by 150m	*nil*	*ns*		**1750-1850**;2000-2150	
" by 200m	*nil*	*ns*		1550-1750;**1750-1950**	
SLOPE by 10°	*50-60 °*	*ns*		10-20°;**20-30°**	
" by 15°	***45-60 °***	*ns*		0-15°	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**NE**	*ns*		*nil*	
" by 90°	**NE**	*ns*		SW or Flat;**NE**	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Rock*	*ns*		*nil*	
" (reclassed)	***Seed***	*ns*		*nil*	
SPECIES GROUP	*Rock;Ponderosa/df;Ponderosa/mix;Dougfir/mix*	*ns*		*nil*	
plant association	*PIPO*	*ns*		*nil*	
CANOPY (orig.)	11-30%	*ns*		*nil*	
" (reclassed)	1-30%	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal *typeface. Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 16	**JENNRICH-TURNER 90% Probability contour**
M *n* = 49	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	***2050-2150***	15.004	7	1450-1550;**1650-1750**;1850-1950	
" by 150m	1250-1400	32.152	5	1400-1550;**1700-1850;1850-2000**	x
" by 200m	-	-		-	
SLOPE by 10°	***60-70 °***	*ns*		**0-10°**	
" by 15°	***60-75 °***	*ns*		*nil*	
" by 30°	***60-90 °***	*ns*		*nil*	
ASPECT by 45°	W or S	*ns*		W or S;**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD; Medium/MS+*	*ns*		*nil*	
" (reclassed)	Unforested	*ns*		*nil*	
SPECIES GROUP	*Ponderosa;Pacificsf/mix;Subalpfir/df;Subalplrch/mix*	*ns*		**Mixed-conifer**	
plant association	PSME	*ns*		**Mixed-conifer**	x
CANOPY (orig.)	*nil*	*ns*		Unforested	
" (reclassed)	Unforested	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 20	**JENNRICH-TURNER 90% Probability contour**
F *n* = 41	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	19.578	7	**1350-1450;...;1550-1650**;1750-1850;1950-2050	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	15.294	8	0-10°;10-20°;**20-30°;30-40°**	
" by 15°	60-75°	17.211	5	0-15°;**15-30°;30-45°**	x
" by 30°	-	-		-	
ASPECT by 45°	**NE**	12.172	4	SW or Flat;W or S;NE or SW;**N or E;NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Rock*	*ns*		*nil*	
" (reclassed)	*Water*	*ns*		*nil*	
SPECIES GROUP	*Rock;Ponderosa;Ponderosa/mix*	*ns*		Lodgepole	
plant association	*PIPO*	*ns*		PICO	
CANOPY (orig.)	1-10%	*ns*		**71-100%**	x
" (reclassed)	-	-		-	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 104090	**JENNRICH-TURNER 90% Probability contour**
M *n* = 39	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	15.90	7	1350-1450;**1650-1750;1850-1950**;1950-2050;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		**0-10°**	
" by 15°	*60-75 °*	*ns*		**0-15°**;15-30°	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**N or E**	*ns*		W or S;**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Rock;Small/MS++*	*ns*		*nil*	
" (reclassed)	Unforested;*Seed*	*ns*		Unforested;**Small**	x
SPECIES GROUP	*Ponderosa;Dougfir/lp;Hardwoods*	*ns*		*nil*	
plant association	*Hardwoods;PIPO*	*ns*		**ABLA2**	
CANOPY (orig.)	1-10%	*ns*		Unforested;71-100%	x
" (reclassed)	-	-		-	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 111167	**JENNRICH-TURNER 90% Probability contour**
F *n* = 93	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*2050-2150*	*ns*		**1650-1750**	
" by 150m	*1250-1400*	*ns*		*nil*	
" by 200m	1950-2150	*ns*		*nil*	
SLOPE by 10°	*50-60 °*	*ns*		**20-30°**	
" by 15°	*60-75 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	SW or Flat	*ns*		*nil*	
" by 90°	NW or SE	*ns*		*nil*	
" by 180°	*nil*	*ns*		*nil*	
STRUCTURE(orig.)	*Small/MS++*	*ns*		**Small/MS-**	
" (reclassed)	*Seed*	*ns*		**Small**	
SPECIES GROUP	*Ponderosa/df;* ***Hardwoods***	*ns*		*nil*	
plant association	PIPO	*ns*		Unforested;Mixed-conifer;PSME;**ABLA2;PICO**	x
CANOPY (orig.)	*1-10%*	*ns*		*nil*	
" (reclassed)	*Water*	9.138	4	Unforested;1-30%;**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*
– *Not tested*		

lynxID 195058 M n = 44	**JENNRICH-TURNER 90% Probability contour** **FINE-SCALE SELECTION (within Home Range)**				
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1950-2050	43.217	6	**1350-1450;...;1450-1550**;1650-1750;1750-1850	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		**0-10°**;10-20°	
" by 15°	***60-75 °***	*ns*		*nil*	
" by 30°	***60-90 °***	*ns*		*nil*	
ASPECT by 45°	**NE**	*ns*		W or S;NW or SE;**N or E;NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		*nil*	
" (reclassed)	*Seed*	*ns*		*nil*	
SPECIES GROUP	*Rock;Wlarch/mix;Pacificsf/mix*	*ns*		*nil*	
plant association	*PIAL*	*ns*		*nil*	
CANOPY (orig.)	1-10%	*ns*		*nil*	
" (reclassed)	Unforested	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 5 *n* = 49	**FIXED KERNAL (LSCV) 90% Probability contour** **MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	*ns*		1350-1450;1450-1550;**1750-1850;...;1950-2050**	x
" by 150m	-	-	-	-	
" by 200m	-	-		-	
SLOPE by 10°	70-80°	*ns*		*nil*	
" by 15°	*nil*	*ns*		*nil*	
" by 30°	60-90°	*ns*		*nil*	
ASPECT by 45°	SW or Flat;**N or E**	*ns*		*nil*	
" by 90°	SW or Flat	*ns*		SW or Flat;**NW or SE**	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Water;Medium/MSLD*	*ns*		Small/MS-	
" (reclassed)	*Water*	*ns*		**Unforested**; Seed; Pole; **Small;** Medium	
SPECIES GROUP	*Other;Water;Wlarch/saf;Hardwoods/mix*	*ns*		**Mixed-conifer**	
plant association	*Water*	4.925	10	**Mixed-conifer**	
CANOPY (orig.)	*Water*	*ns*		**31-50%**	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 6	**FIXED KERNAL (LSCV) 90% Probability contour**
M n = 64	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	13.952	7	1350-1450;1450-1550;**1650-1750;...;1850-1950;** 2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*50-60 °*	*ns*		**10-20°**;20-30°;30-40°	
" by 15°	*45-60 °*	*ns*		**0-15°**;30-45°	
" by 30°	60-90°	5.638	2	**0-30°**;30-60°	x
ASPECT by 45°	SW or Flat	*ns*		W or S;**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD;Medium/MS+*	*ns*		**Small/MS-**	
" (reclassed)	*Water*	*ns*		**Small**	
SPECIES GROUP	*Water;Rock;Subalplrch/mix*	*ns*		*nil*	
plant association	*Water;LALY*	*ns*		*nil*	
CANOPY (orig.)	*Water*	*ns*		**Unforested;**31-50%	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *- Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 11	**FIXED KERNAL (LSCV) 90% Probability contour**
M *n* = 60	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	χ2 α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	53.064	7	1350-1450;...;1550-1650;**1650-1750;...;1850-1950**;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		**0-10°;20-30°**	
" by 15°	*60-75 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	NW or SE	*ns*		*nil*	
" by 90°	NW or SE	*ns*		**SW or Flat**;NW or SE	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD*	42.028	18	Grasses;Pole-sm;Small-md;**Small/MS-**	
" (reclassed)	*Water*	20.169	6	Unforested; Seed; Pole; **Small;** Medium	
SPECIES GROUP	Ponderosa;*Subalplrch/mix*	49.333	28	Dougfir/mix;**Lodgepole;Subalpfir;**Mixed-conifer	x
plant association	*LALY*;PIPO	33.178	10	Unforested;Mixed-conifer;PSME;**ABLA2;PICO**	
CANOPY (orig.)	*Water*	*ns*		1-10%;11-30%;31-50%;**51-70%;71-100%**	
" (reclassed)	*Water*	8.41	4	Unforested;1-30%;**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant χ2 association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 16	**FIXED KERNAL (LSCV) 90% Probability contour**
M *n* = 49	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	22.772	7	1350-1450;**1550-1650;...;1750-1850**;1950-2050;2050-2150	x
" by 150m		-			
" by 200m		-			
SLOPE by 10°	*nil*	26.639	8	**0-10°;10-20°**;20-30°;30-40°	
" by 15°	**0-15°**	27.032	5	**0-15°**;15-30°;30-45°	x
" by 30°		-		-	
ASPECT by 45°	NW or SE;**NE**	*ns*		NW or SE;**NE**	x
" by 90°	-	-	-	-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Small/MS++;Medium/MSLD;Medium/MS+*	*ns*		**Small/MSLD;Small/MS-**Pole;**Small**	
" (reclassed)	*Water*	*ns*			
SPECIES GROUP	*Water;Subalplrch/mix;* ***Hardwoods***	43.485	28	Dougfir/mix;**Lodgepole;Subalpfir**	
plant association	LALY;**Hardwoods**	37.506	10	PSME;**PICO**	x
CANOPY (orig.)	*Water*	*ns*		**Unforested;51-70%**	
" (reclassed)	*Water*	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 111167	**FIXED KERNAL (LSCV) 90% Probability contour**
F n = 93	**MESO-SCALE SELECTION (of Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with α = 0.1	**χ2** α = 0.1	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	62.193	7	1350-1450;...;1550-1650;**1650-1750;...;1850-1950**;1950-2050;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;**20-30°**	
" by 15°	*60-75 °*	*ns*		0-15°;**15-30°**	
" by 30°	*60-90 °*	*ns*		**0-30°**;30-60°	
ASPECT by 45°	SW or Flat	*ns*		*nil*	
" by 90°	**SW or Flat**	*ns*		**SW or Flat;**NW or SE	x
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MSLD*	46.422	18	Pole-sm;**Small**;Small-md;**Small/MS-**	
" (reclassed)	Seed	23.695	6	Unforested; Seed; Pole; **Small;** Medium	x
SPECIES GROUP	Ponderosa; *Subalplrch/mix*	48.671	28	Dougfir/mix;**Lodgepole**;**Subalpfir;**Mixed-conifer	x
plant association	*LALY*	32.743	10	Unforested;Mixed-conifer;PSME;**ABLA2;PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested;**51-70%;71-100%**	
" (reclassed)	*Water*	*ns*		Unforested;1-30%;**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* χ2 *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 5	**FIXED KERNAL (LSCV) 90% Probability contour**
n = 49	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	11.164	7	**1850-1950; 1950-2050**; 2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°;10-20°;**20-30°**	
" by 15°	*60-75 °*	*ns*		**15-30E**;30-45°	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**NW or SE;**N or E	*ns*		**NW or SE;**N or E	x
" by 90°	-	*ns*		-	
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Water;Rock;Medium/MSLD*	*ns*		Small/MS-	
" (reclassed)	*Seed*	*ns*		*nil*	
SPECIES GROUP	*Rock;Ponderosa/df,mix;Subalplrch/mix;* ***Hardwoods***	*ns*		*nil*	
plant association	*LALY*	*ns*		*nil*	
CANOPY (orig.)	*nil*	*ns*		71-100%	
" (reclassed)	71-100%	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *– Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 6	**FIXED KERNAL (LSCV) 90% Probability contour**
M *n* = 64	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1450-1550; 1550-1650	7.337	7	1450-1550; 1650-1750; **1850-1950; 1950-2050**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	***40-50 °***	*ns*		0-10°	
" by 15°	*45-60 °*	*ns*		0-15°;**15-30°**	
" by 30°	***30-60 °***	*ns*		*nil*	
ASPECT by 45°	SW or Flat;**NE**	*ns*		*nil*	
" by 90°	NW or SE	*ns*		**SW or Flat;**NW or SE	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	***Small/MS***++	*ns*		**Small/MS-**	
" (reclassed)	Unforested	*ns*		Unforested;Seed;**Pole;**Small; *Medium*	x
SPECIES GROUP	*Ponderosa/df;Subalpfir/df;Whitebark/mix*	*ns*		*nil*	
plant association	*PIAL*	*ns*		**PICO**	
CANOPY (orig.)	Unforested	*ns*		Unforested;**71-100%**	x
" (reclassed)	-	*ns*		-	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 11	**FIXED KERNAL (LSCV) 90% Probability contour**
M $n = 60$	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1450-1550	13.722	7	1550-1650; 1650-1750; **1850-1950; 1950-2050**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*50-60 °*	*ns*		***20-30°***	
" by 15°	***60-75 °***	*ns*		*nil*	
" by 30°	***60-90 °***	*ns*		*nil*	
ASPECT by 45°	SW or Flat;**NE**	*ns*		*nil*	
" by 90°	**NE**	*ns*		**NE**	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Pole/MS+;Small/MS++*	*ns*		*nil*	
" (reclassed)	*Seed*	*ns*		*nil*	
SPECIES GROUP	*Ponderosa/df;Wlarch/mix;Hardwoods*	*ns*		*nil*	
plant association	*Water*	*ns*		*nil*	
CANOPY (orig.)	*nil*	*ns*		*nil*	
" (reclassed)	Unforested	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 16	**FIXED KERNAL (LSCV) 90% Probability contour**
M *n* = 49	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	***2050-2150***	*ns*		**1650-1750;** 1750-1850; 1850-1950	
" by 150m	1850-2000	10.548	5	**1550-1700**; 1850-2000	x
" by 200m	-	-		-	
SLOPE by 10°	***50-60 °;60-70 °***	*ns*		*nil*	
" by 15°	***60-75 °***	*ns*		***15-30°;30-45 °;45-60 °;60-75 °***	
" by 30°	***60-90 °***	*ns*		*nil*	
ASPECT by 45°	**N or E**	*ns*		W or S;**N or E**	x
" by 90°	-	*ns*		-	
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Water;Medium/MSLD;Medium/MS+*	*ns*		*nil*	
" (reclassed)	Unforested;***Seed***	*ns*		Unforested;***Seed;*** **Pole;Small;Medium**	x
SPECIES GROUP	*Rock;Ponderosa;Pacificsf/mix;Subalpfir/df*	*ns*		**Mixed-conifer**	
plant association	***PIAL***	*ns*		**Mixed-conifer**	
CANOPY (orig.)	Unforested	*ns*		*nil*	
" (reclassed)	Unforested	*ns*		*nil*	

** Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *– Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 111167	**FIXED KERNAL (LSCV) 90% Probability contour**
F *n* = 93	**FINE-SCALE SELECTION (within Home Range)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*2050-2150*	*ns*		*nil*	
" by 150m	*1250-1400*	*ns*		*nil*	
" by 200m	>2100	*ns*		**1600-1850; 1850-2100**; >2100	x
SLOPE by 10°	*50-60 °*	*ns*		*nil*	
" by 15°	***45-60 °***	*ns*		*nil*	
" by 30°	**30-60°**	*ns*		*nil*	
ASPECT by 45°	SW or Flat	*ns*		*nil*	
" by 90°	NW or SE; **NE**	*ns*		*nil*	
" by 180°	*nil*	*ns*		*nil*	
STRUCTURE(orig.)	*Small/MS++;Medium/MS+*	*ns*		**Small/MS-**	
" (reclassed)	Medium	*ns*		Unforested;Seed;**Pole;**Small;Medium	x
SPECIES GROUP	*Ponderosa/df;Ponderosa/lp;WLarch/mix*	*ns*		*nil*	
plant association	*PIPO;* ***Hardwoods***	*ns*		*nil*	
CANOPY (orig.)	*1-10%*	*ns*		*nil*	
" (reclassed)	Unforested	*ns*		*nil*	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns Not significant *– Not tested*	*x Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

Pooled radiolocations (24 lynx)

Single (meso-)scale, seasonal habitat selection: Winter

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	2050-2150	15.114	7	1350-1450; **1750-1850**; **1850-1950**; 1950-2050; 2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		30-40°	
" by 15°	*60-70 °*	*ns*		*nil*	
" by 30°	*60-90 °*	*ns*		**0-30°**; 30-60°	
ASPECT by 45°	**NE**	*ns*		NW or SE	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Medium/MS+*	*ns*		**Small**; Small-md; **Small/MS-**	
" (reclassed)	*Water*	*ns*		Pole; **Small**	
SPECIES GROUP	*Other; Water; Subalplrch/mix*	*ns*		Dougfir/mix; **Lodgepole; Subalpfir**	
plant association	*Water; LALY*	*ns*		PSME; **ABLA2**; **PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested; **71-100%**	
" (reclassed)	*Water*	*ns*		**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* – *Not tested*	× *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

Pooled radiolocations (24 lynx)

Single (meso-)scale, seasonal habitat selection: Summer

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	1350-1450	26.019	7	1350-1450; 1450-1550; **1750-1850; 1850-1950**; 2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		**10-20°**	
" by 15°	*60-70 °*	*ns*		*nil*	
" by 30°	*60-90 °*	*ns*		*nil*	
ASPECT by 45°	**NE**	*ns*		**NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Water; Rock*	*ns*		Pole-sm; Small-md; **Small/MS-**	
" (reclassed)	*Water*	*ns*		**Pole**; **Small**	
SPECIES GROUP	*Water; Rock; Ponderosa/df*	*ns*		Dougfir/mix; **Lodgepole**	
plant association	*Water*	*ns*		PSME; **PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested; **71-100%**	
" (reclassed)	*Water*	*ns*		**71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 5 *n* = 49	**FIXED KERNAL (LSCV) 90% Probability contour** **EXTENDED MESO-SCALE SELECTION (of Home Range within Zone of Availability buffered by mean MDD of 2.38 km)**				
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	<1150; 1150-1250	45.797	11	<1150; ...; ...; 1350-1450; **1650-1750; ...; ...; 1950-2050**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*70-80 °*	*ns*		**10-20°**; 30-40°	
" by 15°	*60-75 °*	*ns*		30-45°	
" by 30°	*60-90 °*	*ns*		**0-30°**; 30-60°	
ASPECT by 45°	SW or Flat	*ns*		*nil*	
" by 90°	SW or Flat	*ns*		SW or Flat; **NW or SE**	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Ag*	*ns*		Small-md; **Small/MS-**	
" (reclassed)	*Water*	*ns*		Unforested; Seed; Pole; **Small;** Medium	
SPECIES GROUP	*Other; Water; Ag*	*ns*		**Lodgepole; Subalpfir**; Hdwds	
plant association	*Water; LALY*	*ns*		Unforested; PSME; **PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested; 31-50%; **51-70%; 71-100%**	
" (reclassed)	*Water*	*ns*		Unforested; **71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 6 — **FIXED KERNAL (LSCV) 90% Probability contour**

M *n* = 64 — **EXTENDED MESO-SCALE SELECTION (of Home Range within Zone of Availability buffered by mean MDD of 2.38 km)**

Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	<1150; 1150-1250	63.182	11	<1150; ...; ...; 1350-1450; **1650-1750; ...; 1850-1950**	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*50-60 °*	14.005	8	**10-20°**; 20-30°; 30-40°	
" by 15°	45-60°	10.117	5	**0-15°**; 30-45°	x
" by 30°	-			-	
ASPECT by 45°	SW or Flat	*ns*		**N or E**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Ag; Medium/MSLD; Medium/MS+*	*ns*		**Small/MS-**; Medium/MS+	
" (reclassed)	*Water*	-		Unforested; Seed; Pole; **Small;** Medium	
SPECIES GROUP	*Other; Ag*	*ns*		**Lodgepole; Subalpfir**	
plant association	*Water; LALY*	*ns*		PSME; **ABLA2; PICO**	
CANOPY (orig.)	*Water*	*ns*		Unforested; 1-10%; 31-50%; **71-100%**	
" (reclassed)	*Water*	-		Unforested; 1-30%; **71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant*
\- *Not tested*
x *Dataset selected as input for Bayes model*

Highlighted text indicates either: (1) a significant $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 11 M $n = 60$	**FIXED KERNAL (LSCV) 90% Probability contour** **EXTENDED MESO-SCALE SELECTION (of Home Range within Zone of Availability buffered by mean MDD of 2.38 km)**				
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	**$\chi 2$** $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*nil*	115.7	11	<1150; ...; ...; ...; 1450-1550; **1650-1750; ...; 1850-1850;** 1950-2050	
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*60-70 °*	*ns*		0-10°; **10-20°; 20-30°**; 30-40°	
" by 15°	*60-75 °*	*ns*		0-15°; **15-30°;** 30-45°	
" by 30°	*60-90 °*	*ns*		**0-30°**; 30-60°	
ASPECT by 45°	NW or SE	*ns*		*nil*	
" by 90°	NW or SE	*ns*		**SW or Flat**;NW or SE	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Ag; Medium/MSLD*	83.338	19	Grasses;Pole;Pole/MSLD; **Small**;Small-md; **Small/MSLD; Small/MS-**	
" (reclassed)	*Water*	41.049	6	Unforested; Seed; Pole; **Small**; Medium	
SPECIES GROUP	*Other; Ag; Ponderosa*	93.743	29	Grasses; Df; Df/mix; **Lodgepole; Subalpfir; Subalpfir/mix;** *Hdwds*	
plant association	*nil*	67.013	10	Unforested; Mixed-conifer; PSME; **ABLA2; PICO**	
CANOPY (orig.)	*Water*	27.606	6	11-30%; 31-50%; **51-70%; 71-100%**	
" (reclassed)	*Water*	24.428	4	Unforested; **1-30%; 71-100%**	

** Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant $\chi 2$ association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 16 M n = 49	**FIXED KERNAL (LSCV) 90% Probability contour** **EXTENDED MESO-SCALE SELECTION (of Home Range within Zone of Availability buffered by mean MDD of 2.38 km)**				
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	<1150; 1150-1250	69.425	11	<1150;...;1250-1350**;1550-1650 ...1750-1850;**1950-2050;2050-2150	x
" by 150m	-	-		-	
" by 200m	-	-		-	
SLOPE by 10°	*nil*	31.711	8	**0-10°; 10-20°**; 20-30°; 30-40°	
" by 15°	**0-15°**	31.602	5	**0-15°;** 15-30°; 30-45°	x
" by 30°	-			-	
ASPECT by 45°	NW or SE; **NE**	*ns*		NW or SE; **NE**	x
" by 90°	-	-		-	
" by 180°	-	-		-	
STRUCTURE(orig.)	*Ag; Medium/MSLD; Medium/MS+*	54.786	19	Grasses; Pole/MSLD**;** Small-md; **Small/MSLD; Small/MS-**	
" (reclassed)	*Water*	25.071	6	Unforested; Seed; Pole; **Small;** Medium	
SPECIES GROUP	Other; *Water; Ag*	72.289	29	Grasses; Dougfir; Dougfir/mix; **Lodgepole; Subalpfir**	
plant association	*Water;* ***Hardwoods*** *; LALY*	58.536	10	Unforested; Mixed-conifer; PSME; **ABLA2; PICO**	
CANOPY (orig.)	*Water*	13.766	6	Unforested; 1-10%; **51-70%; 71-100%**	
" (reclassed)	*Water*	10.74	4	Unforested**; 31-70%; 71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

lynxID 111167	**FIXED KERNAL (LSCV) 90% Probability contour**
F *n* = 93	**EXTENDED MESO-SCALE SELECTION (of Home Range within Zone of Availability buffered by mean MDD of 2.38 km)**

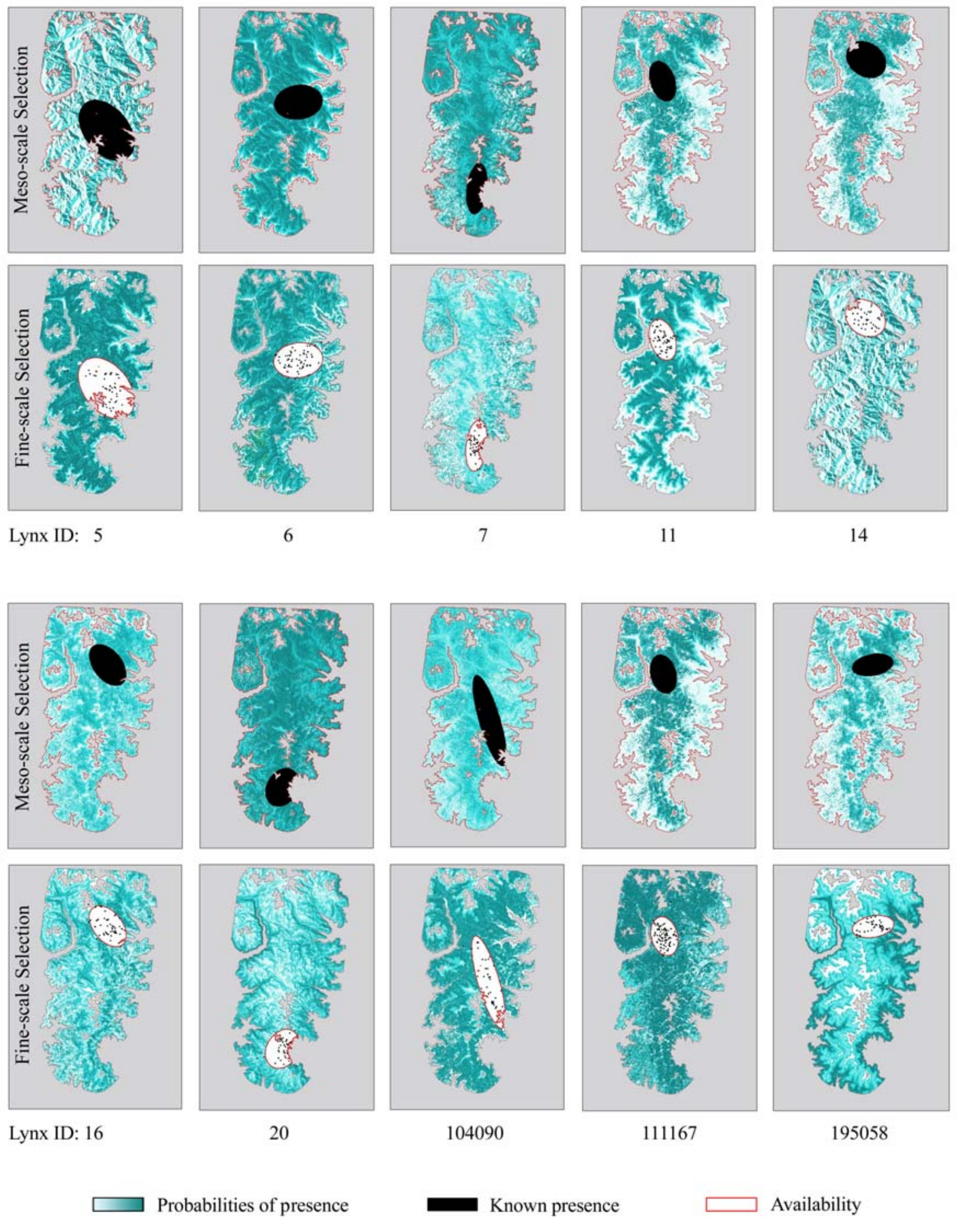
Predictor datasets	**Compositional Analysis*** Classes discriminating Presence/Random with $\alpha = 0.1$	$\chi 2$ $\alpha = 0.1$	df	**Neu's Method*** Classes discriminating Presence/Random within 90% Bonferroni CI	
ELEV'N by 100m	*nil*	128.36	11	<1150; ...; ...; ...; ...; 1550-1650; **1650-1750; ...1850-1950**; 1950-2050	
" by 150m	*nil*	118.62	9	<950;...;...;...;...;1550-1700;**1700-1850;1850-2000**;2000-2150;>2150	
" by 200m	*nil*	104.29	6	<1150; ...; 1350-1550; **1550-1750; 1750-1950;** 1950-2150; >2150	
SLOPE by 10°	*60-70 °*	*ns*		0-10°; **10-20°; 20-30°**; 30-40°	
" by 15°	*60-75 °*	*ns*		0-15°; **15-30°;** 30-45°	
" by 30°	*60-90 °*	*ns*		**0-30°**; 30-60°	
ASPECT by 45°	*nil*	*ns*		*nil*	
" by 90°	NW or SE; **SW or Flat**	*ns*		NW or SE; **SW or Flat**	x
" by 180°	-	*ns*		-	
STRUCTURE(orig.)	*Ag; Medium/MSLD*	89.155	19	Pole-sm; Pole/MSLD; **Small**; Small-md; **Small/MSLD; Small/MS-**	
" (reclassed)	*Water*	45.649	6	*Water*; Unforested; Seed; Pole; **Small**; Medium	
SPECIES GROUP	*Other; Ag*	93.243	29	Grasses; Df; Df/mix; **Lodgepole; Subalpfir; Subalpfir/mix**; Hdwds	
plant association	*Water; LALY*	66.33	10	Unforested; Mixed-conifer; PSME; **ABLA2; PICO**	
CANOPY (orig.)	*Water*	23.656	6	Unforested; 1-10%; **11-30%; 51-70%; 71-100%**	
" (reclassed)	*Water*	20.031	4	Unforested; 1-30%; **71-100%**	

* *Classes for which selection was detected appear in* **bold**. *Classes for which avoidance was indicated appear in* normal typeface. *Classes representing < 1% of all available habitat types appear in italics.*

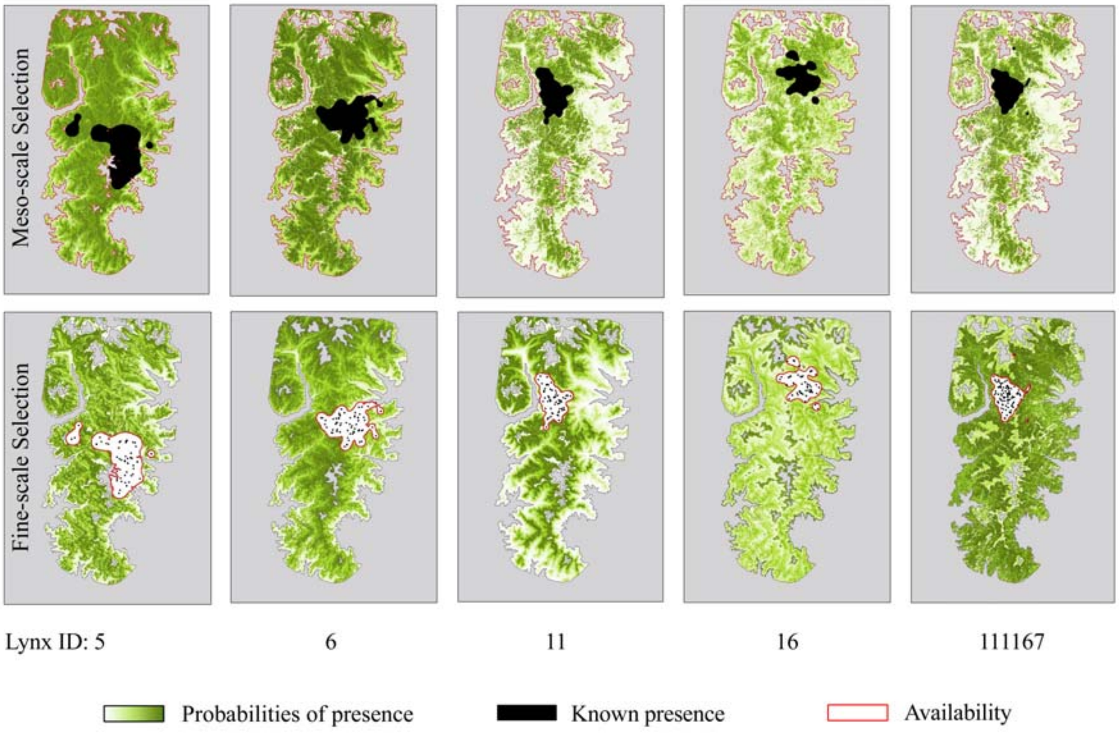
ns *Not significant* - *Not tested*	x *Dataset selected as input for Bayes model*	*Highlighted text indicates either: (1) a significant* $\chi 2$ *association; or, (2) at least one discriminating class composing >=1% of available habitat types.*

APPENDIX E

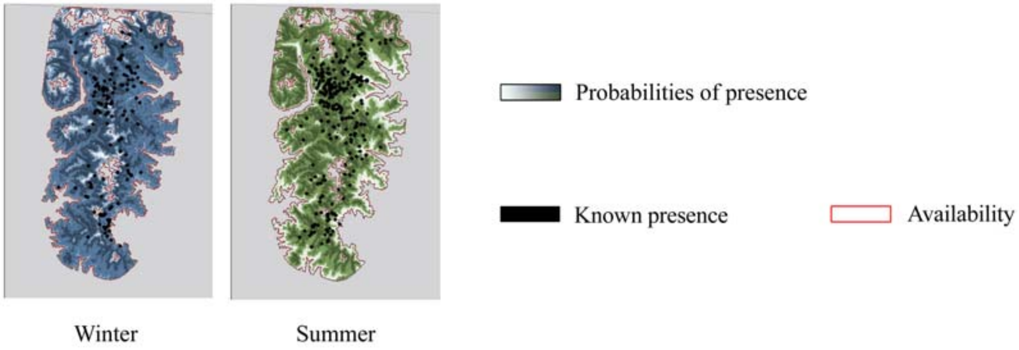
BAYES MODELS



Bayes Models from Selection Scenario 1: The Jennrich-Turner method



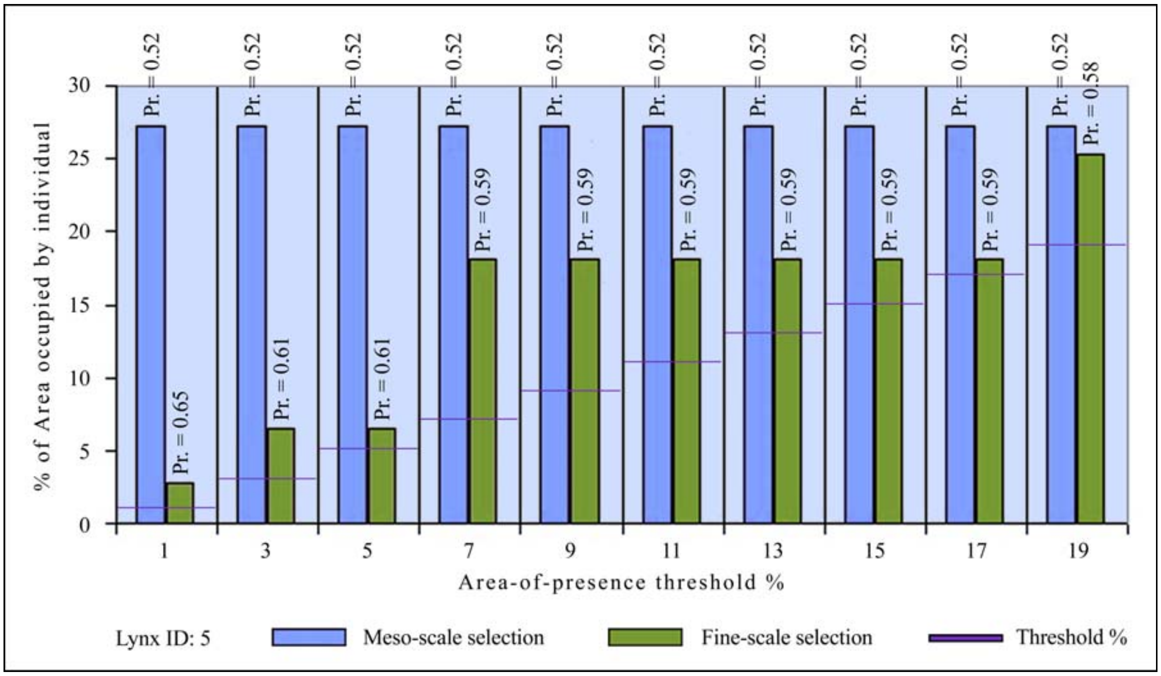
Bayes Models from Selection Scenario 2: The fixed kernal method

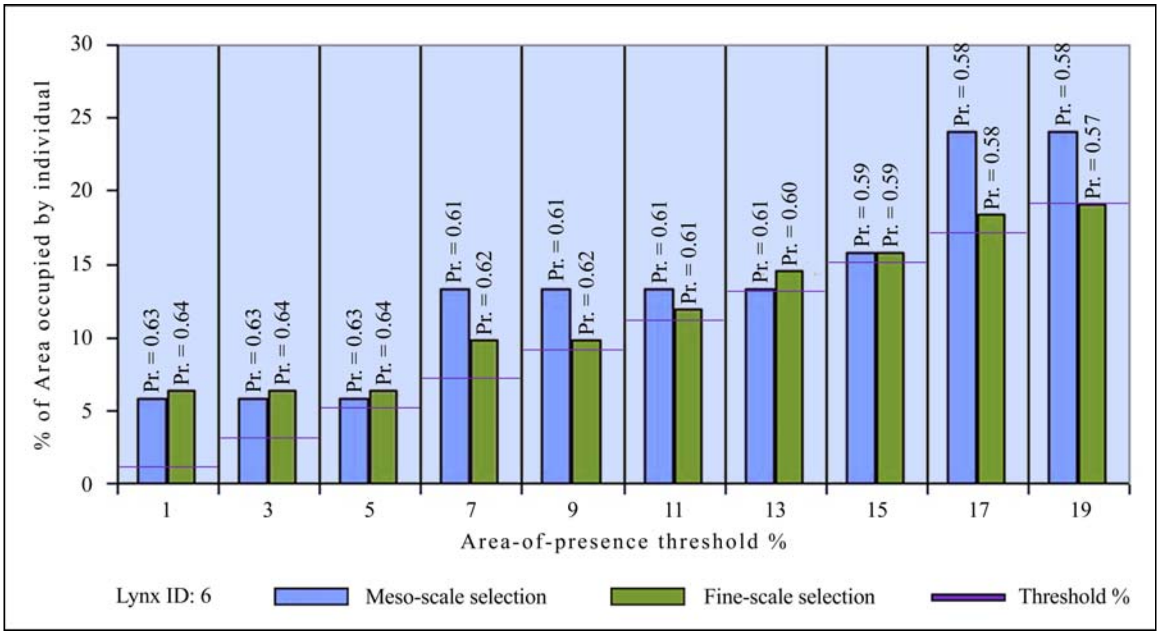


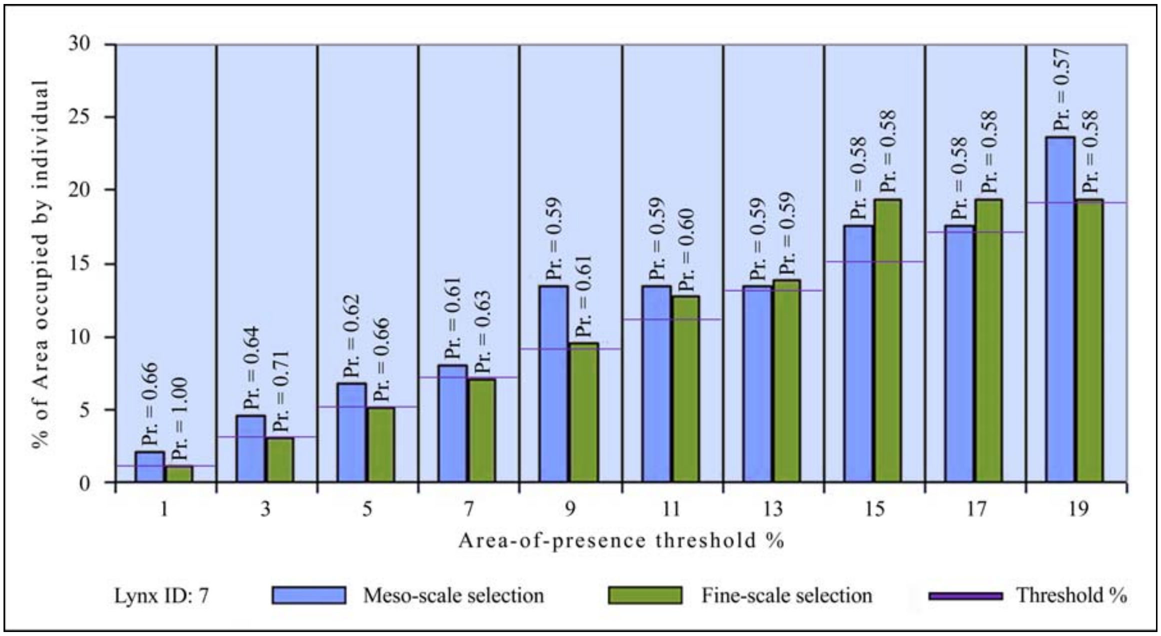
Bayes Models from Selection Scenario 3: Single-scale, by season

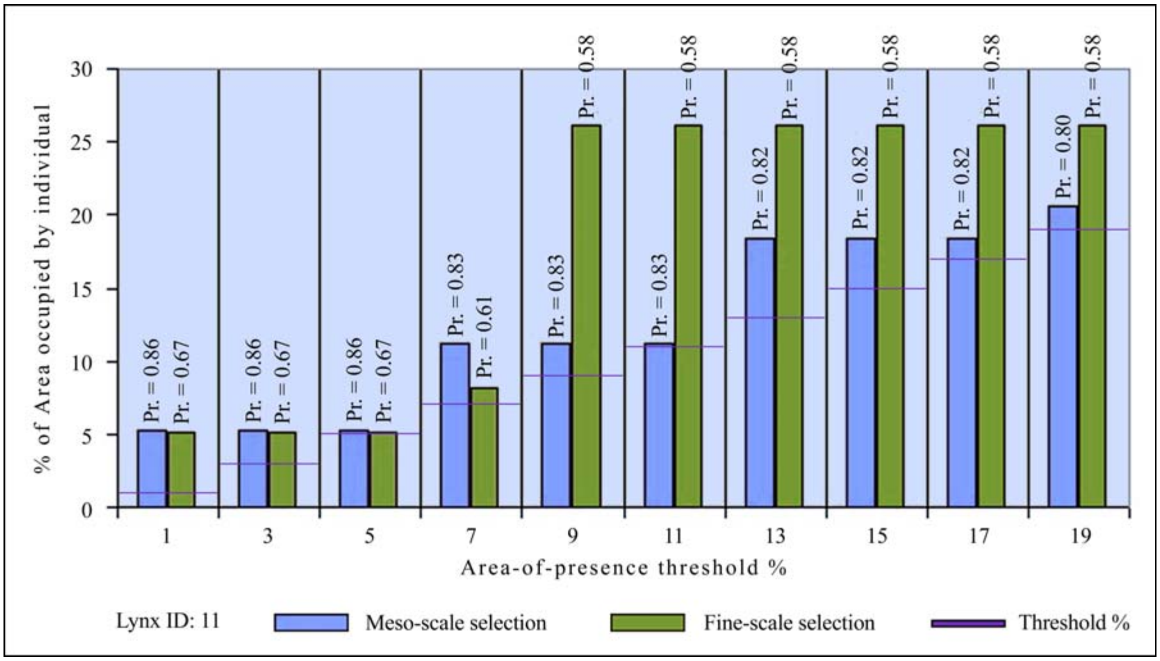
APPENDIX F

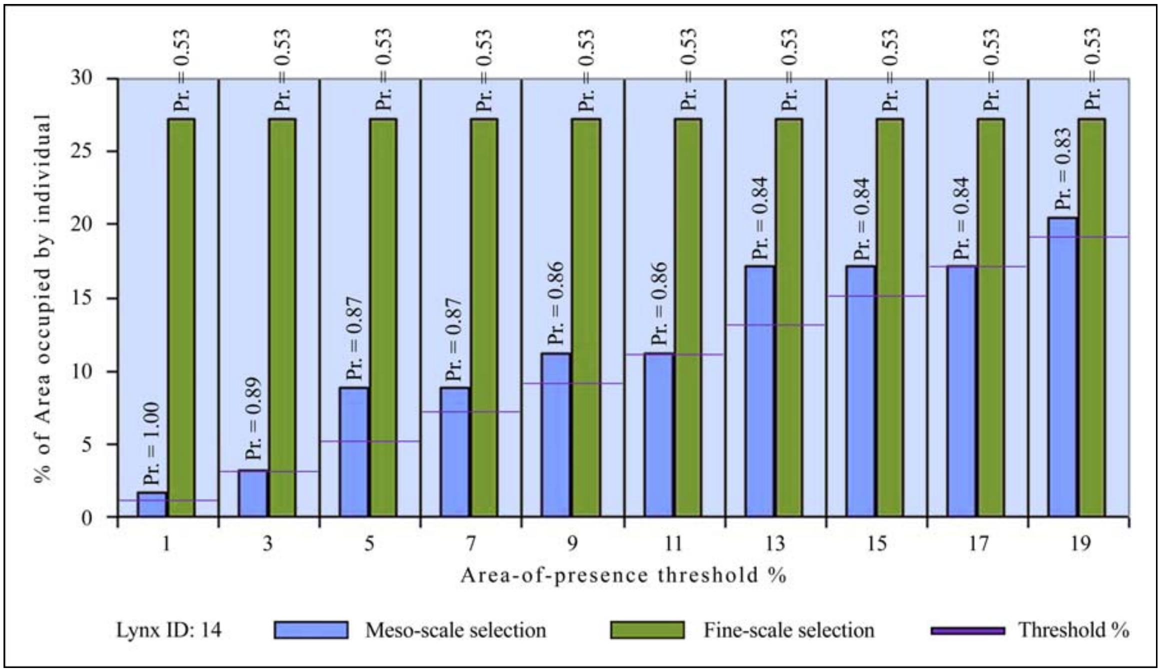
AREAS-OF-PRESENCE


% of Area occupied by individual
0
5
10
15
20
25
30
Pr. = 0.52
Pr. = 0.65
Pr. = 0.52
Pr. = 0.61
Pr. = 0.52
Pr. = 0.61
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.59
Pr. = 0.52
Pr. = 0.58
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 5
Meso-scale selection
Fine-scale selection
Threshold %

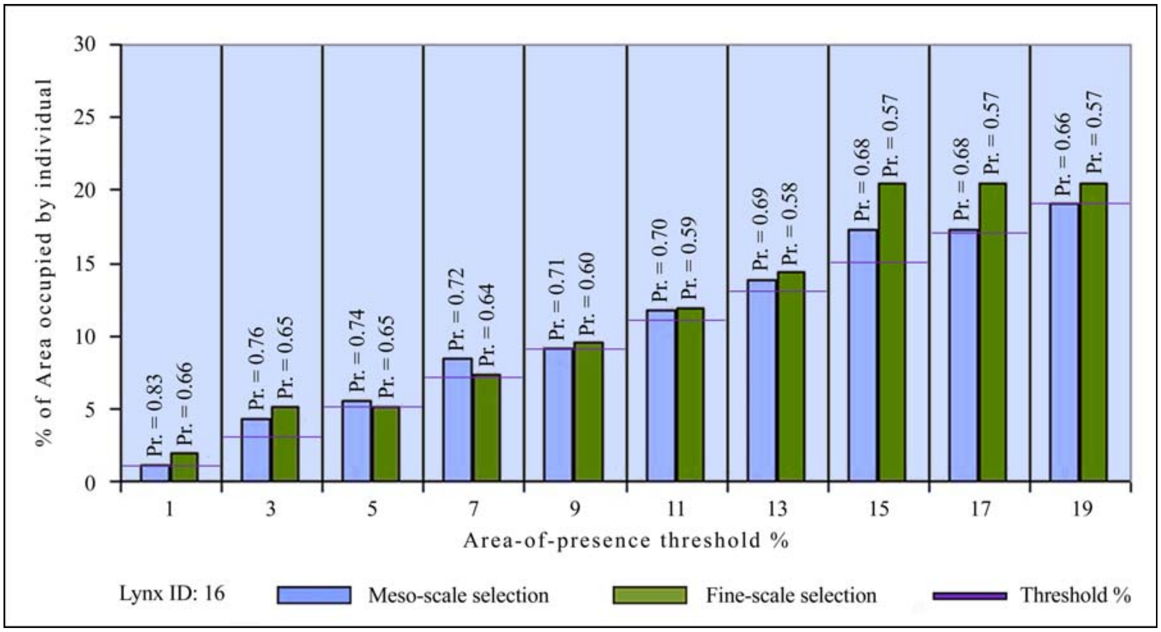

% of Area occupied by individual
0
5
10
15
20
25
30
Pr. = 0.63
Pr. = 0.64
Pr. = 0.63
Pr. = 0.64
Pr. = 0.63
Pr. = 0.64
Pr. = 0.61
Pr. = 0.62
Pr. = 0.61
Pr. = 0.62
Pr. = 0.61
Pr. = 0.61
Pr. = 0.61
Pr. = 0.60
Pr. = 0.59
Pr. = 0.59
Pr. = 0.58
Pr. = 0.58
Pr. = 0.58
Pr. = 0.57
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 6
Meso-scale selection
Fine-scale selection
Threshold %


% of Area occupied by individual
30
25
20
15
10
5
0
Pr. = 0.66
Pr. = 1.00
Pr. = 0.64
Pr. = 0.71
Pr. = 0.62
Pr. = 0.66
Pr. = 0.61
Pr. = 0.63
Pr. = 0.59
Pr. = 0.61
Pr. = 0.59
Pr. = 0.60
Pr. = 0.59
Pr. = 0.59
Pr. = 0.58
Pr. = 0.58
Pr. = 0.58
Pr. = 0.58
Pr. = 0.57
Pr. = 0.58
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 7
Meso-scale selection
Fine-scale selection
Threshold %

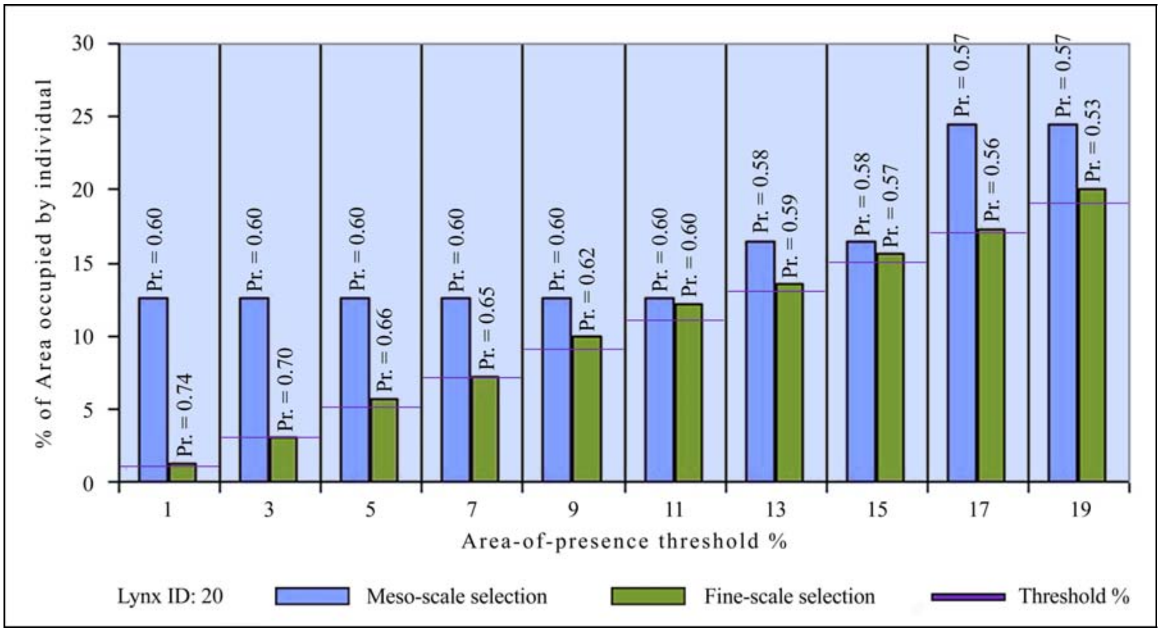

% of Area occupied by individual
30
25
20
15
10
5
0
Pr. = 0.86
Pr. = 0.67
Pr. = 0.86
Pr. = 0.67
Pr. = 0.86
Pr. = 0.67
Pr. = 0.83
Pr. = 0.61
Pr. = 0.83
Pr. = 0.58
Pr. = 0.83
Pr. = 0.58
Pr. = 0.82
Pr. = 0.58
Pr. = 0.82
Pr. = 0.58
Pr. = 0.82
Pr. = 0.58
Pr. = 0.80
Pr. = 0.58
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 11
Meso-scale selection
Fine-scale selection
Threshold %

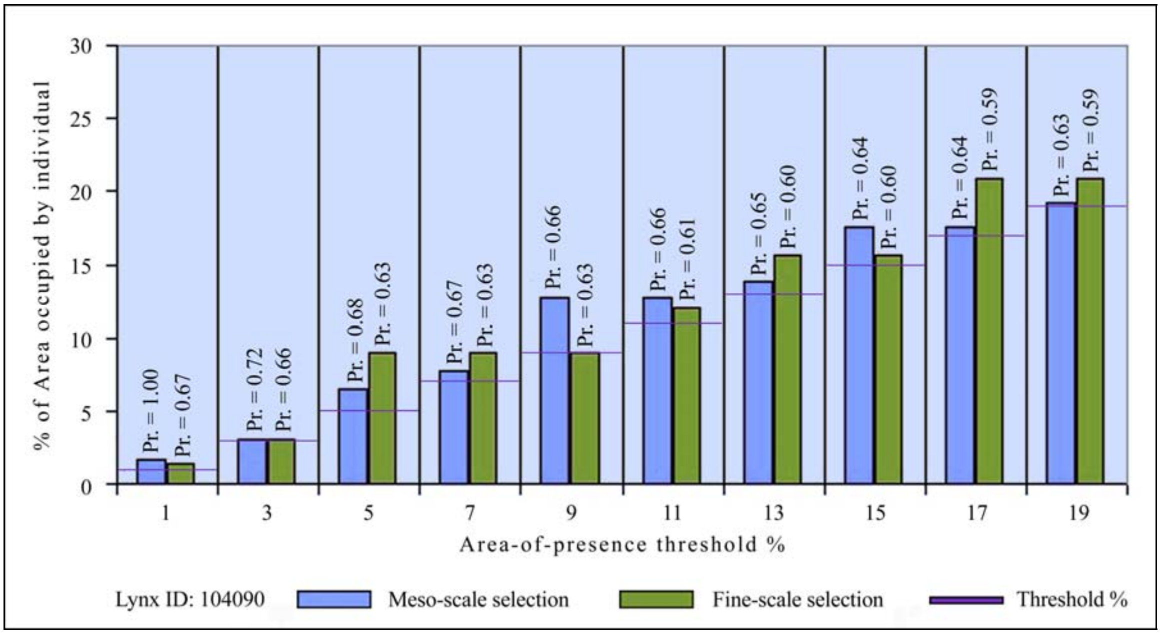


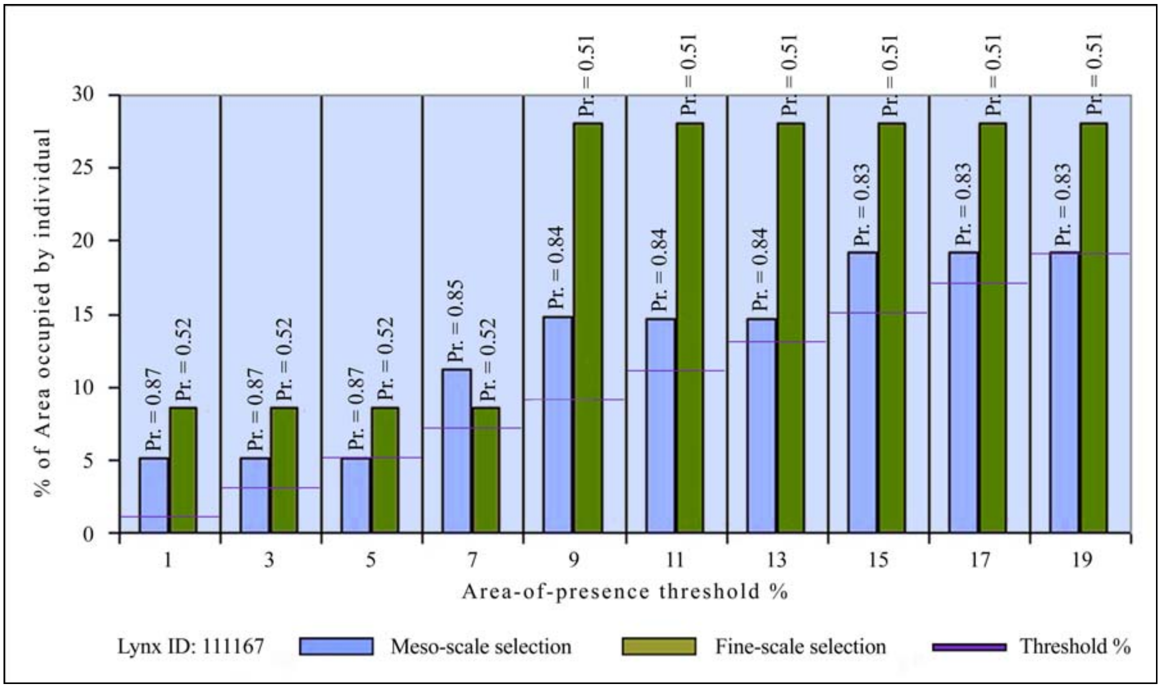
30
25
20
15
10
5
0
% of Area occupied by individual
Pr. = 1.00
Pr. = 0.53
Pr. = 0.89
Pr. = 0.53
Pr. = 0.87
Pr. = 0.53
Pr. = 0.87
Pr. = 0.53
Pr. = 0.86
Pr. = 0.53
Pr. = 0.86
Pr. = 0.53
Pr. = 0.84
Pr. = 0.53
Pr. = 0.84
Pr. = 0.53
Pr. = 0.84
Pr. = 0.53
Pr. = 0.83
Pr. = 0.53
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 14
Meso-scale selection
Fine-scale selection
Threshold %

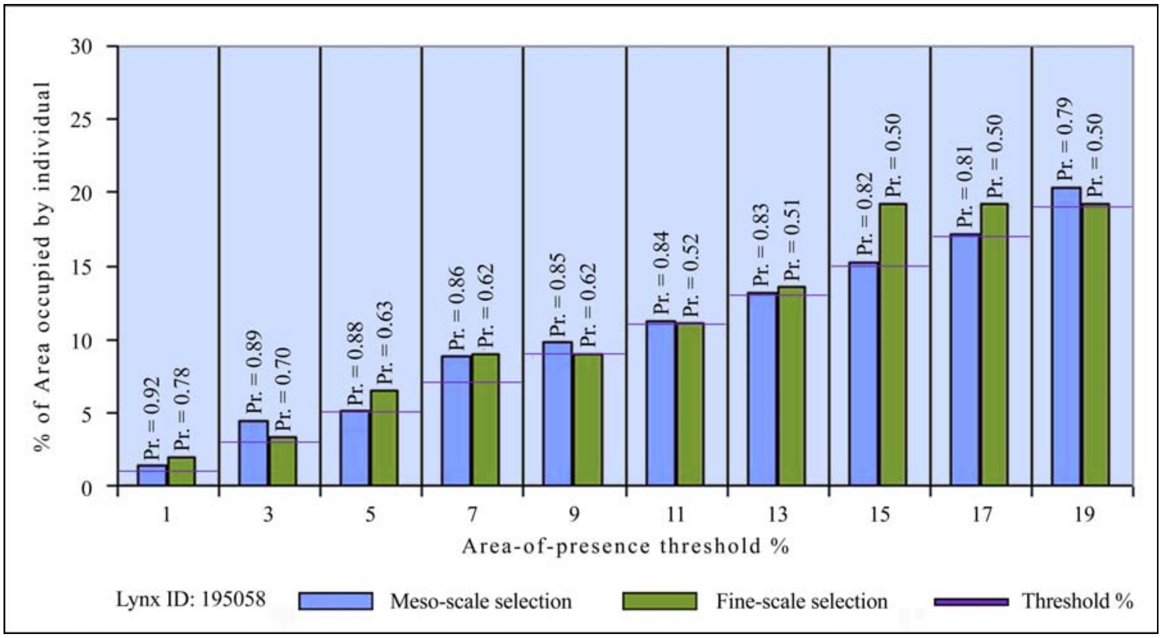


30
25
20
15
10
5
0
% of Area occupied by individual
Pr. = 0.83
Pr. = 0.66
Pr. = 0.76
Pr. = 0.65
Pr. = 0.74
Pr. = 0.65
Pr. = 0.72
Pr. = 0.64
Pr. = 0.71
Pr. = 0.60
Pr. = 0.70
Pr. = 0.59
Pr. = 0.69
Pr. = 0.58
Pr. = 0.68
Pr. = 0.57
Pr. = 0.68
Pr. = 0.57
Pr. = 0.66
Pr. = 0.57
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 16
Meso-scale selection
Fine-scale selection
Threshold %


% of Area occupied by individual
Area-of-presence threshold %
0
5
10
15
20
25
30
1
3
5
7
9
11
13
15
17
19
Pr. = 0.60
Pr. = 0.74
Pr. = 0.60
Pr. = 0.70
Pr. = 0.60
Pr. = 0.66
Pr. = 0.60
Pr. = 0.65
Pr. = 0.60
Pr. = 0.62
Pr. = 0.60
Pr. = 0.60
Pr. = 0.58
Pr. = 0.59
Pr. = 0.58
Pr. = 0.57
Pr. = 0.57
Pr. = 0.56
Pr. = 0.57
Pr. = 0.53
Lynx ID: 20
Meso-scale selection
Fine-scale selection
Threshold %

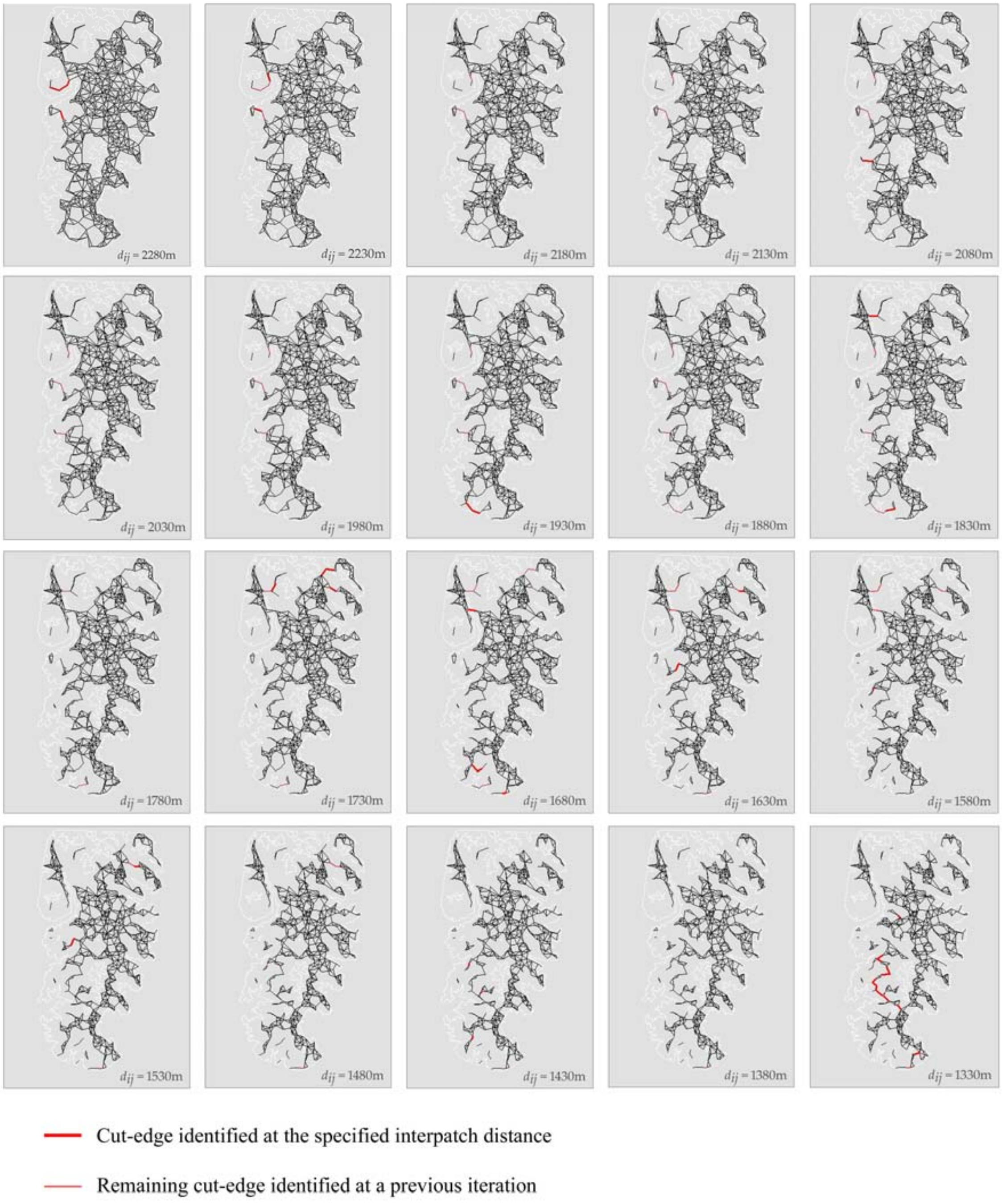

% of Area occupied by individual
Area-of-presence threshold %
0
5
10
15
20
25
30
1
3
5
7
9
11
13
15
17
19
Pr. = 1.00
Pr. = 0.67
Pr. = 0.72
Pr. = 0.66
Pr. = 0.68
Pr. = 0.63
Pr. = 0.67
Pr. = 0.63
Pr. = 0.66
Pr. = 0.63
Pr. = 0.66
Pr. = 0.61
Pr. = 0.65
Pr. = 0.60
Pr. = 0.64
Pr. = 0.60
Pr. = 0.64
Pr. = 0.59
Pr. = 0.63
Pr. = 0.59
Lynx ID: 104090
Meso-scale selection
Fine-scale selection
Threshold %


% of Area occupied by individual
0
5
10
15
20
25
30
Pr. = 0.87
Pr. = 0.52
Pr. = 0.87
Pr. = 0.52
Pr. = 0.87
Pr. = 0.52
Pr. = 0.85
Pr. = 0.52
Pr. = 0.84
Pr. = 0.51
Pr. = 0.84
Pr. = 0.51
Pr. = 0.84
Pr. = 0.51
Pr. = 0.83
Pr. = 0.51
Pr. = 0.83
Pr. = 0.51
Pr. = 0.83
Pr. = 0.51
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 111167
Meso-scale selection
Fine-scale selection
Threshold %

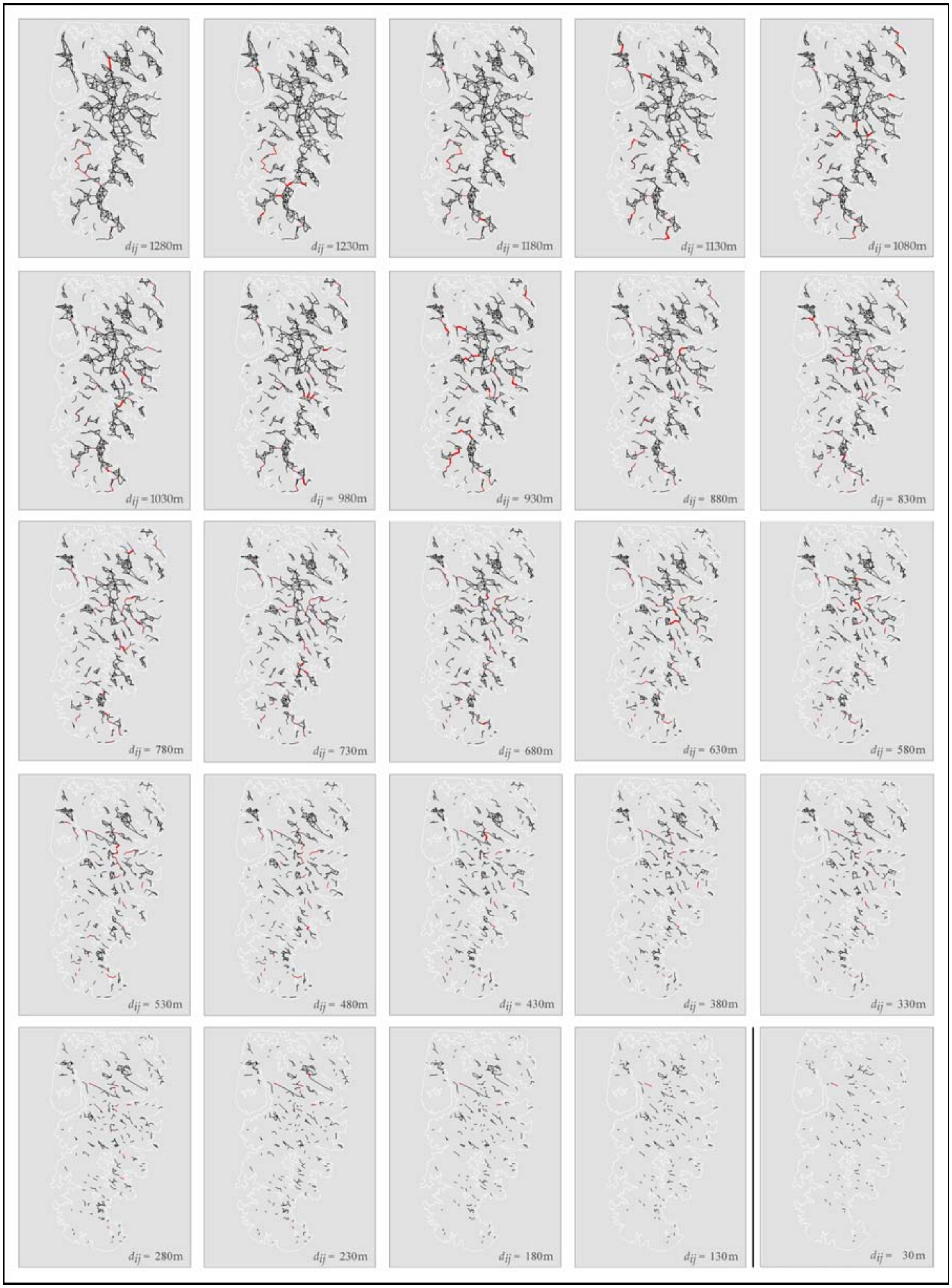

% of Area occupied by individual
0
5
10
15
20
25
30
Pr. = 0.92
Pr. = 0.78
Pr. = 0.89
Pr. = 0.70
Pr. = 0.88
Pr. = 0.63
Pr. = 0.86
Pr. = 0.62
Pr. = 0.85
Pr. = 0.62
Pr. = 0.84
Pr. = 0.52
Pr. = 0.83
Pr. = 0.51
Pr. = 0.82
Pr. = 0.50
Pr. = 0.81
Pr. = 0.50
Pr. = 0.79
Pr. = 0.50
1
3
5
7
9
11
13
15
17
19
Area-of-presence threshold %
Lynx ID: 195058
Meso-scale selection
Fine-scale selection
Threshold %

APPENDIX G

STUDY-WIDE EDGE-THRESHOLDING: AN EXAMPLE FOR ONE GRAPH



Edge-thresholding for the study-wide graph derived from the 7% area-of-presence threshold


d_{ij} = 1280m
d_{ij} = 1230m
d_{ij} = 1180m
d_{ij} = 1130m
d_{ij} = 1080m
d_{ij} = 1030m
d_{ij} = 980m
d_{ij} = 930m
d_{ij} = 880m
d_{ij} = 830m
d_{ij} = 780m
d_{ij} = 730m
d_{ij} = 680m
d_{ij} = 630m
d_{ij} = 580m
d_{ij} = 530m
d_{ij} = 480m
d_{ij} = 430m
d_{ij} = 380m
d_{ij} = 330m
d_{ij} = 280m
d_{ij} = 230m
d_{ij} = 180m
d_{ij} = 130m
d_{ij} = 30m