United States Department of Agriculture

Forest Service

Terrestrial Wildlife Ecology Unit

Washington, D.C.

December 2007

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A suggested citation for this document is as follows:

Beck, J. L., and L. H. Suring. 2007. Description and Evaluation of Frameworks for the Development of Wildlife Habitat–Relationships Models. USDA Forest Service Terrestrial Wildlife Ecology Unit, Washington, D.C., USA. 35 pp.

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Description and Evaluation of Frameworks for the Development of Wildlife Habitat–Relationships Models[1]

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ABSTRACT: Wildlife habitat–relationships models were first developed in the mid-1970s to provide practitioners with tools to evaluate habitat quality. The purpose of our review was to identify and describe the structure, uses, output, and operation of major habitat–relationships modeling frameworks. We defined frameworks as conceptual modeling structures such as modeling shells and general modeling approaches within which models are constructed that are similar in purpose and function. These frameworks provide the foundation for building models for a wide array of animals in almost any environmental setting. We also provide a descriptive analysis of frameworks to assist practitioners in selecting approaches that fit specific operational objectives. We identified 40 frameworks (13 through the 1980s, 12 in the 1990s, and, 15 since 2000) and grouped them according to 10 nominal- and 5 ordinal-scale criteria. The proportion of frameworks that are not components of larger landscape modeling systems and that use input data readily available in natural resource agency inventories declined from 1980 through 2006. The proportion of frameworks that examine habitat relationships at multiple scales, link scales when multi-scaled, and that are spatially explicit increased from the 1980s through 2006. The proportion of frameworks that have received scientific credibility through publication or application of results, or other mechanisms has remained above 0.83, but the proportion of frameworks where output from at least 1 model developed within a framework has been validated with field data never exceeded 0.58. We used agglomerative hierarchical cluster methods to identify groupings of habitat–relationships modeling frameworks based on dissimilarity distance between each framework according to criteria ratings. CompPATS and HABSCAPES did not meet our cluster grouping criteria, but the remaining 38 frameworks were apportioned among 7 clusters, each containing an average of 5.4 (range = 2–10) frameworks. Each cluster was characterized by specific strengths and limitations that practitioners should assess prior to selecting a framework that best meets their modeling objectives. Cluster 1 included HSI and 9 other frameworks that were based on species-habitat matrices or newly emerging analysis techniques. Cluster 2 was characterized by frameworks that were components of larger landscape modeling systems. Cluster 3 approached habitat modeling through modeling shells, GIS-based modeling systems, or a diversity of other techniques to model habitat relationships. Frameworks in Cluster 4 use simple approaches to evaluate habitat quality, often developed for use within a GIS. Both frameworks in Cluster 5 link multiple-scales to evaluate habitat quality. Frameworks in Cluster 6 predict changes in habitats. Frameworks in Cluster 7 provide predictive tools that are useful in assessing impacts of land management activities on species and habitats. Our evaluation provides conceptual information for practitioners evaluating how well wildlife habitat–relationships frameworks may achieve modeling objectives. To assist

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[1] This manuscript is a prepublication version of Beck and Suring (2008)
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developers of future wildlife habitat–relationships modeling frameworks, we provide insights to the development of rigorous, yet practical frameworks that follow current trends in wildlife–habitat relationships modeling and suggestions to overcome limitations in existing frameworks.

KEY WORDS: habitat modeling, habitat-population linkage, habitat suitability modeling, spatial relationships, wildlife-habitat relationships modeling

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INTRODUCTION

Habitats are areas of land that provide resources such as food, cover, and water and environmental conditions such as precipitation and soil types that affect occupancy of individuals or populations of species, allowing those species to survive and reproduce (Morrison et al. 2006). Changing requirements in the 1970s to evaluate and report the effects of land management activities on wildlife habitats and associated populations led to a need for new analysis techniques. Wildlife habitat–relationships models were first developed in the mid-1970s (Salwasser et al. 1980) to provide practitioners with tools to evaluate habitat quality for selected species. The underlying goal of many habitat–relationships modeling frameworks is to evaluate habitat quality for wildlife populations, which was described by Hall et al. (1997:178) as "the ability of the environment to provide, conditions appropriate for individual and population persistence."

Habitat capability models have been described as providing an estimate of the area within which resources for a modeled species can be found, or ranking an area based on the capability of that area to support a species based on a few important environmental variables (Morrison et al. 2006:337). Habitat effectiveness models rank resources in an area to the degree that maximum use or carrying capacity can be met (Morrison et al. 2006:337), with effectiveness often tempered to reflect the constraints of human activities on the area actually usable by animals (Lyon and Christensen 1992, Merrill et al. 1999). Throughout this manuscript we generally refer to habitat–relationships modeling frameworks, while recognizing that frameworks have been developed under a variety of structures including species-habitat matrices, habitat suitability, habitat capability, and habitat effectiveness (Morrison et al. 2006). We define frameworks as conceptual modeling structures including modeling shells (e.g., expert systems) and general modeling approaches (e.g., artificial neural networks, Bayesian belief networks, spatial optimization) within which models are constructed that are similar in purpose and function.

Two general approaches have developed to assess habitat quality for wildlife populations. Under species-habitat matrix frameworks, the starting point is a classification of vegetation within which, each classification unit is assigned a value describing its value as habitat for one or more wildlife species (Morrison et al. 2006). Frameworks that use guilds often are structured as a species-habitat matrix, because guilds represent aggregates of species needs typically including generalizations of habitat needs. Work by Thomas (1979) in the Blue Mountains of northeastern Oregon and southeastern Washington, Hoover and Willis (1984) in Colorado forests, and DeGraaf et al. (1992) in New England forests are classic examples of species-habitat matrix modeling frameworks. The second approach to modeling wildlife habitat quality includes frameworks that begin with the habitat requirements of a species and then quantifies these requirements through specific vegetation and other variables to evaluate how an area provides the various required requirements. The Habitat Evaluation Procedures (HEP) developed by the U.S. Fish and Wildlife Service (1981) established the underpinnings for this approach from which many other modeling frameworks have been developed.

Habitat assessments with HEP are based on habitat units, which are products of habitat quality determined by a habitat suitability index (HSI) model and the total area of cover types used by a modeled species (U.S. Fish and Wildlife Service 1981). The basis of an HSI is to quantify an organism's life history requirements (e.g., food and cover) using measurable components of habitat (e.g., vegetation structure, composition, and spatial arrangement). The model structure assumes a direct linear relationship between the value of the HSI and carrying capacity (U.S. Fish and Wildlife Service 1981). For a given evaluation, individual habitat suitability indices for life history requirements are scored by comparison to optimum conditions; individual indices are then typically computed as geometric means to devise HSI models (U.S. Fish and Wildlife Service 1981).

Habitat–relationships modeling frameworks have increased in number and complexity since the mid-1970s. Consequently, selecting a modeling framework to match the objectives of a wildlife conservation program that appropriately consider data availability and the analytical abilities of practitioners can be difficult. The purpose of our review was to describe the structure, uses, output, and operation of wildlife habitat–relationships modeling frameworks to provide practitioners with a basis for selecting frameworks for use. Our specific objectives were to: (1) identify wildlife habitat–relationships modeling frameworks that are currently available for use and (2) provide a descriptive analysis of frameworks to assist practitioners in selecting approaches to modeling wildlife–habitat relationships that best fit their objectives.

METHODS

Identifying and Rating Habitat–Relationships Modeling Frameworks

To focus our search for modeling frameworks we bounded our definition of wildlife habitat–relationships modeling frameworks with 4 criteria that were based on the modeling objectives of each framework. We: (1) considered frameworks that were designed to evaluate habitat for terrestrial wildlife species; (2) considered frameworks that have the potential for multi-species applications, thus avoiding approaches designed solely for 1 species (e.g., Gutiérrez et al. 1992); (3) avoided statistical modeling techniques (e.g., logistic regression, discriminant function analysis, resource selection functions) designed to quantify selection of habitat by a species, although we considered modeling frameworks that incorporate statistical or other analytical concepts to describe habitat relationships (e.g., artificial neural networks, Bayesian belief networks, expert systems, fuzzy logic, spatial optimization); and (4) only considered frameworks that were operational, avoiding those that are currently being conceptualized or were otherwise incomplete.

In many cases, the recently developed wildlife–habitat relationships frameworks we identified were improvements of earlier, more general frameworks. For instance, several newer frameworks including ArcHSI (Juntti and Rumble 2006), HABIT@ (McGarigal and Compton 2003), HCI (McComb et al. 2002), HQI (Rickel 1997), Landscape HSI (Larson et al. 2003, 2004; Dijak et al. 2007, Rittenhouse et al. 2007), and LMS (Marzluff et al. 2002) retain elements of the original 1981 HSI framework, but provide more sophistication through incorporation of advancements such as GIS and spatially explicit analyses. Consequently, we retained newer frameworks that were built on the platforms of older frameworks as independent observations because their advancements allow them to function in different ways than the previously described frameworks. In other cases, frameworks in our analyses were stand-alone, not based on previously described frameworks. To be consistent, however, in each case we adhered to the 4 criteria to identify frameworks according to their modeling objectives.

After identifying the major habitat–relationships modeling frameworks that fit the above 4 criteria we rated each according to 10 nominal- and 5 ordinal-scale criteria to quantify our evaluation (Table 1). Nominal criteria included: 1) whether the breadth of application of the framework could consider a wide range of species in a wide range of environments or was limited to certain taxa or a single environment; 2) whether the frameworks linked habitat conditions with population demographics or surrogates; 3) whether the frameworks were included in comprehensive landscape modeling systems; 4) availability of input data; 5) whether at least 1 individual species model based on a particular framework had been validated with field data; 6) capability of frameworks to examine habitat relationships at single or multiple scales; 7) whether multi-scaled frameworks required linkage information among scales to function; 8) whether the frameworks had attained scientific credibility through publication or application of results suggesting acceptance by an array of professionals; 9) the spatial application of the framework (i.e., does the framework use geographic data [spatial framework]; does the framework examine spatial relationships in habitat data at specific locations or coordinates [spatially explicit]; or, does the framework not rely on geographic or spatial data [aspatial]); and 10) whether vegetation and its attributes were applied in the framework as the basis for a species-habitat matrix or as variables to assess habitat relationships for wildlife species (Table 1). Ordinal criteria included: 1) whether documentation was adequate to clearly understand and apply the modeling frameworks; 2) ease of application; 3) whether output was well defined and measurable; 4) whether frameworks were well-suited for the scales they were developed to examine; and 5) transparency of the frameworks' structure (Table 1). We conducted two independent reviews of each framework and then reached consensus on criteria ratings that differed.

Table 1. Nominal- and ordinal-scale criteria used to rate wildlife habitat–relationships modeling frameworks.

Criteria	Definition	Rating scale
Nominal criteria		
Breadth of application	Can the framework be used to define habitat relationships for a wide range of species in a wide range of environments?	0 = only suited for a single species or environment 1 = suited for a wide range of species in a wide range of environments
Habitat–population linkage	Does the modeling framework incorporate vital rates (e.g., production, survival), other demographic parameters (e.g., density, population size); surrogates (e.g., quality of home ranges, habitat conditions in critical reproductive habitats, presence/absence) of population demographic parameters; or does the modeling framework model habitat conditions without specific consideration of wildlife population parameters?	0 = does not rely on population demographics or surrogates of modeled species 1 = relies on surrogates for population demographic parameters or framework can utilize population demographics if desired, but is not dependent on them 2 = specifically relies on population demographics of modeled species

Table 1. Nominal- and ordinal-scale criteria used to rate wildlife habitat–relationships modeling frameworks.

Criteria	Definition	Rating scale
Independence	Is the framework part of a larger landscape modeling system?	0 = a component of a larger landscape modeling system 1 = stands alone and is not part of a larger landscape modeling system
Input requirements	Is the required input data (e.g., GIS coverages, stand and wildlife inventory data) readily available in agency inventories?	0 = not readily available 1 = readily available
Model validation	Has output from at least 1 model developed within a framework been validated with field data?	0 = no validation known or validation impossible 1 = model validated
Scale application	Is the framework limited to 1 scale or can it explicitly examine differences in habitat conditions at a range of spatial scales?	1 = limited to 1 scale 2 = capable of examining habitat conditions at more than 1 scale (e.g., forest and region)
Scale linkage	If the framework is multi-scaled, are the scales linked?	0 = scales are not linked 1 = scales are linked
Scientific credibility	Has the framework gained credibility through publication of results, application of results, or other mechanisms to suggest acceptance by an array of professionals?	0 = limited credibility 1 = at least 1 publication of results using this framework, or other application of the modeling framework
Spatial application	Does the framework: not rely on geographic data (aspatial); examine geographic data (spatial framework); or examine spatial relationships in habitat data at specific locations or coordinates as part of its structure (spatially explicit)?	1 = aspatial 2 = spatial 3 = spatially explicit
Vegetation application	How does the framework apply vegetation and its attributes in modeling?	0 = applied as the basis for a wildlife species-habitat matrix 1 = applied as habitat variables to assess wildlife–habitat relationships
Ordinal criteria		
Documentation	Is there sufficient documentation (e.g., a user's manual or website) to clearly understand the modeling framework?	0 = limited 1 = marginal 2 = sufficient
Ease of application	Is the model difficult to parameterize, run, and understand the output?	1= difficult 2 = moderate 3 = easy
Output definition	Is the output well defined and will it translate to something that can be measured?	1 = difficult 2 = moderate 3 = easy
Scale definition	Is the framework well suited for the scales it is defined to examine?	0 = not well-suited 1 = moderately well-suited 2 = very well-suited
Transparency	Is the structure of the framework clear (i.e., is the flow of the framework apparent)?	1 = difficult 2 = moderate 3 = easy

Description of Habitat–Relationships Modeling Frameworks

To depict trends in development of wildlife habitat–relationships modeling frameworks we plotted nominal criteria as proportions across the 3 decades encompassing our review (1980s, 1990s, and 2000s), with the final decade covering 2000–2006. Because California wildlife habitat relationships (Salwasser et al. 1980), pattern recognition (Williams et al. 1977), and wildlife habitat quality (Roller 1978) modeling frameworks were developed in the mid- to late 1970s, we included these frameworks with those described in the 1980s. We developed narratives for each framework summarizing the origins of the framework, capabilities of the framework including data inputs and outputs, and related information (e.g., availability of software).

We conducted cluster analyses to better understand relationships among frameworks and to identify frameworks with similar characteristics. We used agglomerative hierarchical cluster methods to identify groupings of habitat–relationships modeling frameworks based on dissimilarity distance between each framework (PROC CLUSTER; SAS Institute 2003). Our input data for cluster analyses were the criteria ratings for each framework. Because our ratings consisted of nominal and ordinal data, we computed Gower's similarity coefficients (Gower 1971) between each pair of frameworks. We then computed Gower's dissimilarity coefficient (1 – Gower's similarity coefficient) in PROC DISTANCE (SAS Institute 2003) to base clustering on heterogeneity within the data ratings between frameworks. We used the average linkage cluster method, which is an unweighted pair-group method that uses arithmetic averages of dissimilarity coefficients to compute distance between clusters (PROC CLUSTER; SAS Institute 2003). We used an R^2-type measure of total within-cluster heterogeneity to evaluate the proportion of variance accounted for by joining each cluster. When each framework is in a cluster by itself, $R^2 = 1$ because there is no within-cluster variability; as frameworks are grouped into clusters, within-cluster variability increases from 0 and R^2 decreases from 1. We plotted R^2 values for each cluster in a hierarchical tree diagram (PROC TREE; SAS Institute 2003) and used a cutoff value of $R^2 = 0.60$ to define cluster groupings. We computed Gower's dissimilarity coefficients within each identified cluster group to evaluate within-cluster variability and report the mean and range in these coefficients for each cluster (PROC MEANS; SAS Institute 2003). Because Gower's dissimilarity coefficients range from 0 to 1, higher values indicate greater within-cluster heterogeneity. Lastly, we described attributes of each cluster group to better understand common patterns.

RESULTS

Identifying and Rating Habitat–Relationships Modeling Frameworks

Based on our review of known frameworks and interpretation of documentation available to us we identified n = 40 modeling frameworks (Table 2). We located 13 frameworks developed through the 1980s, 12 frameworks developed in the 1990s, and 15 developed since 2000. Ten (0.25) frameworks exist within a larger landscape assessment system (ALCES, BOREAL, CompPATS, EMDS, HCI, LEAM, LEEMATH, LMS, SESI, and SIMFOR). Although HCI was developed as a component of the Coastal Landscape Analysis and Modeling System (CLAMS; Spies et al. 2002), it can model wildlife–habitat relationships outside of this system (B. C. McComb, University of Massachusetts, personal communication, 2006). Eight (0.20)

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
A Landscape Cumulative Effects Simulator (ALCES)	ALCES quantifies economic contributions of land use practices, identifies associated environmental and industrial issues, and assists in development of mitigation strategies. The availability and quality of habitat for specific wildlife species is determined by tracking the area and area weighted value of different vegetation and landscape types.	Schneider et al. 2003, ALCES 2005
Animal, Landscape and Man Simulation System (ALMaSS)	ALMaSS predicts the effect of changing landscape structure or management on key wildlife species. It incorporates detailed species-specific life history information and is agent-based, allowing each individual to interact with other individuals and the environment.	Topping et al. 2003
Artificial Neural Network (ANN)	Neural network models are inspired by natural physiology and mimic the neurons and synaptic connections of the brain. Once trained for a given task, a network can be applied by providing suitable data on the network inputs. Published applications used habitat variables to model nesting habitat for red-winged blackbirds, marsh wrens, and northern bobwhite quail.	Özesmi and Özesmi 1999, Lusk et al. 2002, Özesmi et al. 2006
Arc-Habcap	Arc-Habcap is a deterministic GIS-based wildlife habitat model that originated from a spreadsheet-based habitat capability (Habcap) model. The model in Benkobi et al. (2004) predicts effectiveness of forage, cover, and cover-forage proximity, as well as effects of roads, on elk distributions. The Arc-Habcap framework can be used to model habitat for any terrestrial vertebrate based on association with vegetation structural stages.	Benkobi et al. 2004
Arc Habitat Suitability Index (ArcHSI)	ArcHSI is a GIS-based model that estimates the ability of an area to meet the food and cover requirements of an animal species. The components and parameters of the model occur in tables and can be easily edited or otherwise modified. ArcHSI runs on personal computers with the full installation of ArcGIS.	Juntti and Rumble 2006
Bayesian Belief Networks (BBN)	BBNs depict probabilistic relations among variables and use Bayesian statistics to calculate probabilities of outcomes, such as population presence, given conditions of input variables (e.g., condition of habitat).	Marcot et al. 2001, Raphael et al. 2001, Marcot 2006

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
Biodiversity Expert System Tool (BEST)	BEST uses data from the U.S. Geological Survey's Gap Analysis Program (GAP) and other data in a GIS environment. This tool provides predictions of conflict between proposed land uses and biotic elements and is intended for use at the start of a development review process.	Crist et al. 2000
BIRDHAB	BIRDHAB is a wildlife habitat relationships model developed for national forests in the Southern Region to assist in assessment of proposed management actions. It is written as an ArcInfo GIS program that accesses stand inventory data and a species-habitat matrix to describe the relative quality of habitat for 271 species of birds.	U.S. Forest Service 1994, Kilgo et al. 2002
BOREAL	BOREAL is a tactical planning decision support system that predicts the effects of alternative forest management strategies on forest product yields, revenues, and habitat area and distribution. This framework uses readily available inventory data and provides tabular, graphical, and map output.	Puttock et al. 1998
Computerized Project Analysis and Tracking System (CompPATS)	CompPATS evaluates the effects of forest management on wildlife habitat, sedimentation, visual quality, timber yield, and net revenue. Wildlife values describe habitat capacity, not an estimate of animal abundance.	Ouachita National Forest 1988, Keller et al. 1994
California Wildlife Habitat Relationships (CWHR)	CWHR is maintained by the California Department of Fish and Game. Habitat suitability indices may be calculated for land use planning assessments using GIS and fuzzy logic.	Salwasser et al. 1980, Raphael and Marcot 1986, Block et al. 1994, California Department of Fish and Game 2005
Effective Area Model (EAM)	EAM is an empirically based spatial model that incorporates patch size and shape, composition of matrix habitats, and species-specific edge responses to predict the organization of animal assemblages occupying heterogeneous landscapes. Specifically, it predicts the effects of matrix habitats on species abundances in habitat patches.	Sisk et al. 1997, Brand et al. 2006

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Framework	Description	Primary references
Ecosystem Management Decision Support (EMDS)	EMDS v. 2.0 is an application framework for knowledge-based decision support of ecological assessments that is designed for use at any geographic scale. The system integrates GIS and knowledge-based reasoning technologies in the Microsoft Windows® environment.	Reynolds (1999a, b); Reynolds (2001), Stoms et al. (2002)
Expert Systems	Expert systems are a formalized method of organizing and applying information and opinion which utilize quantitative information when available, but usually rely primarily on expert opinion. Results may be expressed in terms of conditional states or probabilities.	Marcot 1986
FORHAB	FORHAB is a deciduous forest stand simulation model that may be used to predict changes in available breeding habitat for birds.	Smith et al. 1981
HABIT@	Habitat@ evaluates habitat at multiple, interconnected scales through indices that represent the quality of selected variables with numerous options for summarizing, combining, and/or comparing model variables (e.g., arithmetic mean, product, geometric mean, minimum).	McGarigal and Compton 2003
HABSCAPES	HABSCAPES uses spatial databases to map the predicted occurrence of all terrestrial vertebrate and aquatic amphibian species relative to landscape pattern over large geographic areas. Spatial databases describing the landscape are linked to databases containing wildlife habitat relationships and life history characteristics using custom FORTRAN programs and PARADOX scripts.	Huff et al. 2001; Mellen et al. 1995, 2001
HABSIM	HABSIM tracks vegetation seral stages, quantifies the change in vegetation structure and composition for each seral stage over time, and relates this information to potential carrying capacity for the species of interest.	Raedeke and Lehmkuhl 1986
Habitat-Based Species Viability (HBSV) Model	With HBSV, areas of high quality habitat for a species are assumed to support individuals in smaller home ranges, with higher rates of survival, and with higher reproductive success. The number of individual home ranges of different quality habitat for an individual species are mapped and quantified to assess the potential viability of the species.	Roloff and Haufler 1997, 2002

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
Habitat Capability Index (HCI)	HCI estimates the capability of a landscape patch and its surrounding neighborhood to provide conditions important to a species survival and reproduction. These values are based on vegetation and physical conditions over a range of scales on the landscape.	McComb et al. 2002, Spies et al. 2002
Habitat Effectiveness Index (HEI)	HEI originated through the development of models to evaluate cumulative effects and is computed as the difference between analogues of death and birth rates, which yields a measure of habitat suitability. An index of human activity may be used as an analogue of death rates. An index of habitat quality, potentially described by vegetation, food availability, and abiotic factors is often used as an analogue of birth rate.	Thomas et al. 1988, Merrill et al. 1999
Habitat Quality (HQ)	The HQ framework measures habitat interspersion (Is) and juxtaposition (Jx) through GIS processes and incorporates it with limiting factors (RDF) that are essential for the species of interest. The form of the relationship is $HQ = (0.2*Is/8) + (0.6*Jx/12) + (0.2*RDF)$ resulting in values from 0.0 to 1.0.	Roy et al. 1995
Habitat Quality (HQI) and Habitat Quality Plus (HQI+)	This is a GIS (ArcView) PC application that was developed to provide information for development of forest plans (HQI for single species analyses; HQI+ for multiple species analyses). An index value from 0.0 to 1.0 is assigned to habitat patches based on cover type, canopy, tree size, and season.	Rickel 1997
Habitat Suitability Index (HSI)	HSI indices are a composite (often a geometric mean) of individual suitability index (SI) scores reflective of habitat variables that represent cover types, life requisites, and life stages for habitats of individual species, each scaled 0 (unsuitable habitat) to 1 (optimum habitat). SI scores range from 0 to 1 and are computed as a ratio of a value of interest (i.e., estimate or measure of habitat conditions) divided by a standard of comparison (i.e., optimum habitat condition). HSI models assume a linear relationship between the index value and carrying capacity for the species of interest.	U.S. Fish and Wildlife Service 1981

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
Landscape HSI	Landscape HSI applies a 0–1 habitat suitability index to large landscapes through the use of GIS-based modeling of raster data (e.g., tree species and age) across entire landscapes. Landscape HSI has also incorporated other programming to facilitate evaluation of spatially explicit landscape attributes (e.g., LANDIS) and wildlife population fitness parameters (e.g., RAMAS).	Larson et al. 2003, 2004; Shifley et al. 2006, Dijak et al. 2007, Rittenhouse et al. 2007
Land Use Evolution and Impact Assessment Model (LEAM)	The LEAM model determines the location of habitat patches likely to sustain populations of species of interest, estimates population size, and assesses the degree of connectivity and potential gene flow between patches. When applied to a changing landscape, the results of the model indicate changes in species-specific patch connectivity and determine the impact of land-use change on population isolation and habitat fragmentation.	Aurambout et al. 2005
Landscape Evaluation Effects of Management Effects on Timber and Habitat (LEEMATH)	LEEMATH is a spatially and temporally explicit tool that integrates habitat attributes, habitat suitability, stand growth, spatial habitat attributes, and landscape characteristics. Model input is a management regime defined by a timber harvest schedule, a silvicultural treatment plan, the spatial distribution of stands, and the target wildlife species. Outputs include timber growth and harvest (e.g., total basal area), habitat attributes (e.g., mean habitat patch size) and habitat suitability (e.g., total habitat area).	Li et al. 2000
Landscape Management System (LMS)	LMS is a computerized system that integrates landscape-level spatial information, stand-level inventory data, and distance-independent individual tree growth models to project changes through time in tree growth and snag decay across forested landscapes. Management scenarios are evaluated in terms of wildlife habitat and timber revenue.	Marzluff et al. 2002
Program to Assist in Tracking Critical Habitat (PATCH)	PATCH is a spatially explicit, individual-based, life history simulator designed to project populations of territorial terrestrial vertebrate species through time. Inputs include habitat maps, specifications for habitat use (territory size and habitat affinity), vital rates (survival and reproduction), and descriptions of species' movement behavior. Outputs include spatial estimates of habitat occupancy rate and source-sink characteristics.	Schumaker 1998, Schumaker et al. 2004

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
Pattern Recognition (PATREC)	PATREC is a modeling framework that relies on Bayesian statistical inference which requires that habitat conditions be expressed as conditional probabilities (i.e., 1 or more of the habitat conditions under consideration is much more probable [occurs more frequently] than the others). Expected densities of animals can be computed based on knowledge of densities and habitat conditions.	Williams et al. 1977, Grubb 1988
Point Specific Estimator (PSE)	PSE estimates quality of habitat from single variable data bases (e.g., vegetation maps) in terms of interspersion, juxtaposition, and spatial diversity. Input requirements include cover type and values of cover types to wildlife species. Outputs for raster-based maps are possible through application of the spatial diversity index values to each grid cell.	Mead et al. 1981, Lyon et al. 1987
RAMAS Landscape	RAMAS Landscape integrates the LANDIS landscape model with the RAMAS GIS habitat-based metapopulation model to provide predictions about the viability, recovery, and growth of species based on predicted changes in landscapes.	Akçakaya et al. 2004, 2005
Spatially Explicit Species Index (SESI)	SESI models are similar to HSI models in that population response is predicted by a set of habitat relationships and in that habitat quality is quantified by an index value. However, SESI models can focus either on one part of a life cycle, such as breeding or foraging, or whole life cycles. They incorporate temporal changes in the environment, can be used to model the responses of any species in the system, and provide a landscape index map rather than just a single index or set of indices.	Curnutt 2000
SIMFOR	SIMFOR evaluates the response of forest vegetation to management or natural disturbances, and calculates potential landscape and wildlife habitat conditions. By matching wildlife species requirements with projected habitat attributes, SIMFOR estimates species-specific habitat suitability. Simple landscape metrics based on seral stage, patch size and edge characteristics are also calculated.	Wells et al. 1999, Wells and May 2002, Seely et al. 2004

Table 2. Summary of 40 habitat–relationships modeling frameworks.

Framework	Description	Primary references
Spatially-Neutral Bayesian Model (SNBM)	The simplest potential distribution of a wildlife species is a random distribution where all sites have equal probabilities. A more ecologically appropriate potential spatial distribution accounts for environmental variation. This expected distribution is called a spatially-neutral model, because it is generated without hypothesizing spatial factors that regulate the distribution of resources or organisms.	Milne et al. 1989
Spatial Optimization	Spatial optimization is not a habitat modeling framework, *per se*, but provides a framework within which the results of habitat modeling may be applied to obtain habitat configurations to best meet specific management objectives. Optimization of landscapes aims to identify landscape and land use patterns, which support certain ecosystem functions in an optimal way. The chosen performance criteria are based upon the ecosystem functions considered for optimization.	Hof and Bevers 1998
Species-area Relationship (SPPAREA)	Species-area curves are computed as $S = cA^z$, where S = number of species, c = a constant that varies with taxon and geographic region, A = area, and z = a constant measuring the slope of the line relating S and A. Species-habitat area relationships were first explored on islands, but have been extended to a wide variety of habitats.	Schroeder 1996
Species-Habitat Matrices (SHM)	Species-habitat matrices are databases used to predict the presence or relative abundance of species within geographic areas or within sera1 stages of vegetation types. More detailed predictions include ratings for life requisites of species such as reproduction, feeding, and cover. Most species-habitat matrices rely on previously published information and expert opinion as the basis for their entries.	Thomas 1979, Hoover and Willis 1984, DeGraaf et al. 1992, Scott et al. 1993, Karl et al. 2000
Species Sorting Algorithm (SSA)	SSA derives data from a spatial landscape analysis and from published species life-histories to evaluate the full suite of species that could occur on a landscape. The SSA identifies and concentrates attention on species that have, due to ecological factors such as habitat specificity or negative response to management activities, the potential to be affected by proposed land management.	Reed et al. 2001; Higdon et al. 2005, 2006

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Framework	Description	Primary references
Wildlife Habitat Quality (WHQ)	WHQ generates numerical ratings of habitat quality based on an analysis of digital habitat maps and associated information. Information on vegetation and terrain (as they affect availability of food and cover), habitat interspersion, and habitat juxtaposition are integrated to provide a score from 0 to 100 to quantify habitat quality.	Roller 1978

frameworks (Arc-Habcap, BEST, BIRDHAB, CompPATS, CWHR, HABSCAPES, PATCH, and SHM) apply vegetation and its attributes as the basis for evaluating wildlife–habitat relationships within species-habitat matrices.

Since development of wildlife–habitat relationship models began, most frameworks have defined habitat relationships for a wide range of species in a wide range of environments (Fig. 1A). During the 1990s, more (0.33) frameworks applied vegetation attributes within the context of species-habitat matrices than other decades (Fig. 1B). The proportion of frameworks that are not components of larger landscape modeling systems (Fig. 1C) and that use input data that are typically readily available in natural resource agency inventories declined from 1980 through 2006 (Fig. 1D). The proportion of frameworks that examine habitat relationships at multiple scales (Fig. 2A), link scales when multi-scaled (Fig. 2B), and that are spatially-explicit (Fig. 2C) increased from the 1980s through 2006. The proportion of frameworks that use population demographics or surrogates generally increased from the 1980s through 2006 (Fig. 2D). Over time, the proportion of frameworks where at least one species model based on that framework has been validated through comparing predictions to observed data, reserving data to use in validation, or other techniques has never exceeded 0.58 (Fig. 3A), but the proportion of frameworks that have received scientific credibility through peer-reviewed publication or application of results, or other mechanisms has consistently remained >0.83 (Fig. 3B).

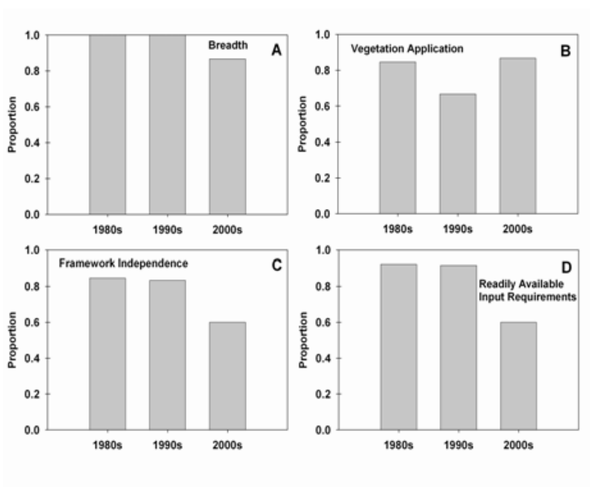

Figure 1. Proportion of wildlife habitat–relationships modeling frameworks developed by decade (A) suited for a wide range of species in a wide range of environments, (B) where vegetation was applied as habitat variables to assess wildlife–habitat relationships, (C) that are stand alone frameworks, not a component of a landscape modeling system, and (D) with input requirements that are readily available in agency inventories.

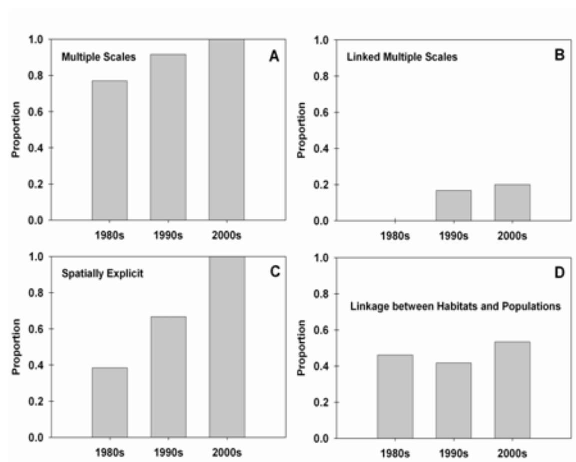

Figure 2. Proportion of wildlife habitat–relationships modeling frameworks developed by decade, which (A) examine habitat relationships at multiple scales, (B) provide linkage between scales if multi-scaled, (C) are spatially explicit and (D) use population demographics or surrogates of population demographics to model habitat relationships.

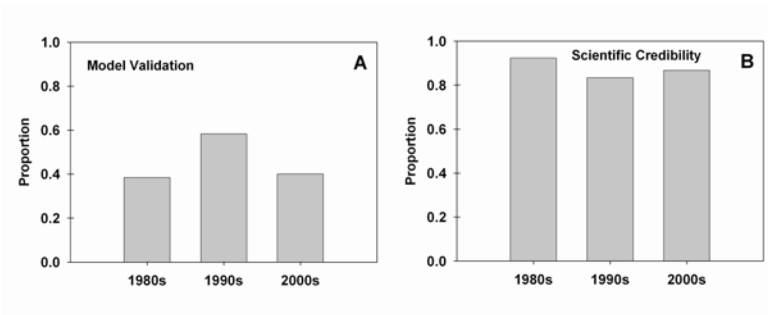

Figure. 3. Proportion of wildlife habitat–relationships modeling frameworks developed by decade (A) where at least 1 model developed within that framework has been validated with field data, (B) that have attained scientific credibility through publication of results, application of results, or other mechanisms to suggest acceptance by an array of professionals.

Description of Habitat–Relationships Modeling Frameworks

Only 2 (0.05) frameworks (ALMaSS and LEEMATH) were limited to a single environment (Table 3). Of the total, 3 (0.08) frameworks were aspatial (Expert Systems, HABSIM, CompPATS; Table 3). Four (0.10; ANN, CompPATS, SPPAREA, and WHQ) of the reviewed frameworks considered habitat relationships at a single spatial scale (Table 3). Five of the 36 (0.14) multi-scale frameworks (BBN, HABIT@, HCI, EMDS, and PATCH) provided linkage between scales (Table 3). Nineteen (0.48) frameworks incorporated population demographics or surrogates into modeling. Twenty-seven (0.68) frameworks have the ability to incorporate spatially explicit characteristics (Table 3).

Total heterogeneity between CompPATS, HABSCAPES and other frameworks was $R^2 \geq 0.60$, indicating these 2 frameworks were different from other frameworks based on our criteria so they were not included in any clusters (Fig. 4). Heterogeneity was lowest between frameworks for the cluster formed by HEI and HBSV ($R^2 = 1.000$) and highest ($R^2 = 0.000$) between CompPATS, HABSCAPES, and all clusters (Fig. 4). Thirty-eight frameworks were apportioned within 7 clusters, each cluster containing an average of 5.4 (range = 2–10) frameworks. Mean dissimilarity between all modeling frameworks was 0.352 (range: 0.034–0.753), indicating average heterogeneity was low-to-moderate, yet the range in heterogeneity between frameworks was broad.

Cluster 1.—Cluster 1 consisted of HSI and 9 other frameworks ($R^2 = 0.739$) that rely on emerging analysis techniques (ANN, CWHR, HEI, HBSV, PATCH, and PATREC) and/or evaluate wildlife–habitat relationships within the context of species-habitat matrices (Arc-Habcap, BIRDHAB, CWHR, PATCH, and SHM; Fig. 4; Table 3). Mean dissimilarity between all frameworks was 0.241 (range: 0.071–0.429), indicating that frameworks within the cluster were rather similar in their characteristic abilities (i.e., how they fit our evaluation criteria). Input for all frameworks in Cluster 1 was readily available in natural resource agency inventories. Output was easy to define and measure for all frameworks in Cluster 1 (Table 3). Species-specific models for each framework in Cluster 1 have been validated, each framework was suited for a wide range of species in a wide range of environments, and has attained scientific credibility (Table 3). Among the 3 largest clusters, Cluster 1 was highest (0.70) for frameworks that relied on population demographics or surrogates. All frameworks in Cluster 1

Table 3. Ratings for criteria used to assess wildlife habitat–relationships modeling frameworks.

	Nominal criteria[a]										Ordinal criteria[b]				
Framework	Breadth	Habitat pop-link	Indep	Input req	Model valid	Scale	Scale link	Credible	Spatial appl	Veg appl	Document	Ease	Output	Scale def	Trans
Cluster 1															
ANN	W	S	I	RA	V	S	NL	C	S	HV	S	M	E	VWS	D
Arc-Habcap	W	S	I	RA	V	M	NL	C	SE	SHM	L	M	E	VWS	E
BIRDHAB	W	No	I	RA	V	M	NL	C	S	SHM	S	E	E	VWS	E
CWHR	W	S	I	RA	V	M	NL	C	S	SHM	S	M	E	VWS	M
HBSV	W	S	I	RA	V	M	NL	C	SE	HV	S	M	E	VWS	E
HEI	W	S	I	RA	V	M	NL	C	SE	HV	S	E	E	VWS	E
HSI	W	No	I	RA	V	M	NL	C	S	HV	S	E	E	MWS	E
PATCH	W	S	I	RA	V	M	L	C	SE	SHM	S	M	E	VWS	E
PATREC	W	S	I	RA	V	M	NL	C	S	HV	S	E	E	VWS	E
SHM	W	No	I	RA	V	M	NL	C	S	SHM	S	M	E	MWS	E
Cluster 2															
ALCES	W	No	NI	NRA	NV	M	NL	C	SE	HV	S	M	M	VWS	D
BOREAL	W	No	NI	RA	NV	M	NL	C	S	HV	L	D	M	VWS	D
EMDS	W	No	NI	RA	NV	M	L	C	SE	HV	S	D	E	VWS	D
HCI	W	No	NI	RA	V	M	L	C	SE	HV	S	M	E	VWS	M
LEAM	W	S	NI	NRA	NV	M	NL	C	SE	HV	M	M	M	VWS	M
LEEMATH	S	No	NI	NRA	V	M	NL	C	SE	HV	M	D	E	VWS	D
LMS	W	No	NI	RA	V	M	NL	C	SE	HV	S	D	E	VWS	M
SESI	W	No	NI	RA	V	M	NL	C	SE	HV	M	D	M	VWS	M
SIMFOR	W	No	NI	RA	V	M	NL	C	SE	HV	S	M	E	VWS	D
Cluster 3															
EAM	W	P	I	RA	V	M	NL	C	SE	HV	M	M	E	VWS	M
Expert Systems	W	No	I	RA	NV	M	NL	C	A	HV	S	M	E	VWS	M

Table 3. Ratings for criteria used to assess wildlife habitat–relationships modeling frameworks.

	Nominal criteria[a]										Ordinal criteria[b]				
Framework	Breadth	Habitat pop-link	Indep	Input req	Model valid	Scale	Scale link	Credible	Spatial appl	Veg appl	Document	Ease	Output	Scale def	Trans
HABSIM	W	P	I	RA	NV	M	NL	C	A	HV	M	M	E	VWS	M
HQ	W	No	I	RA	NV	M	NL	C	SE	HV	M	E	E	VWS	M
Landscape HSI	W	No	I	RA	NV	M	NL	C	SE	HV	S	E	E	VWS	E
RAMAS Landscape	W	P	I	RA	NV	M	NL	C	SE	HV	S	M	E	VWS	D
SNBM	W	S	I	RA	V	M	NL	C	SE	HV	M	D	E	VWS	D
Spatial Optimization	W	S	I	RA	NV	M	NL	C	SE	HV	S	D	E	VWS	D
SPPAREA	W	No	I	RA	NV	S	NL	C	SE	HV	S	E	E	VWS	E
WHQ	W	No	I	RA	NV	S	NL	C	SE	HV	M	M	M	VWS	M
Cluster 4															
ArcHSI	W	No	I	RA	NV	M	NL	NC	SE	HV	S	E	E	MWS	E
HQI	W	No	I	RA	NV	M	NL	NC	S	HV	S	E	M	MWS	M
PSE	W	No	I	RA	NV	M	NL	C	SE	HV	S	M	D	MWS	D
Cluster 5															
BBN	W	S	I	NRA	V	M	L	C	SE	HV	S	E	E	VWS	M
HABIT@	W	S	I	RA	NV	M	L	NC	SE	HV	S	E	M	VWS	M
Cluster 6															
BEST	W	S	I	RA	NV	M	NL	C	S	SHM	L	M	M	MWS	M
FORHAB	W	S	I	NRA	NV	M	NL	C	S	HV	M	D	E	MWS	D
Cluster 7															
ALMASS	S	P	I	NRA	NV	M	NL	C	SE	HV	S	D	E	VWS	M
SSA	W	P	I	NRA	NV	M	NL	C	SE	HV	M	M	M	MWS	E
Non-clustered frameworks															
HABSCAPES	W	No	I	NRA	NV	M	NL	NC	SE	SHM	S	D	E	VWS	D
COMPATS	W	No	NI	RA	NV	S	NL	NC	A	SHM	S	E	M	MWS	D

[a]Definitions for nominal criteria ratings:

Breadth of application (Breadth) = suited for a single species or one environment (S) or for a wide range of species in a wide range of environments (W).
Habitat–population linkage (Habitat pop-link) = does the framework rely on population demographic parameters (P), surrogates of population demographic parameters (S), or does not rely on population demographics or surrogates (No) of modeled species.
Independence (Indep) = framework is independent of (I) or a part of a larger landscape modeling system (NI).
Input requirements (Input req) = not readily available (NRA) or readily available (RA) in agency inventories.
Model validation (Model valid) = at least 1 model based on each framework not validated (NV) or validated (V) with field data.
Scale = is the framework limited to 1 scale (S) or is it capable of examining habitat relationships at more than one scale (M).
Scale linkage (Scale link) = scales in multi-scaled frameworks are not linked (NL) or linked (L).
Scientific credibility (Credible) = framework has gained credibility (C) or not (NC) through publication or application of results.
Spatial application (Spatial appl) = Does the framework: solely examine aspatial (A) data, evaluate geographic data (spatial [S], or examine spatial relationships in habitat data at specific locations or coordinates as part of its structure (spatially explicit [SE]).
Vegetation application (Veg appl) = within the framework, vegetation is applied as the basis for a wildlife species-habitat matrix (SHM) or vegetation is applied as habitat variables that are used to assess habitat relationships for wildlife species (HV).

[b]Definitions for ordinal criteria ratings:

Documentation (Document) = is documentation limited (L), marginal (M), or sufficient (S) to understand the modeling framework.
Ease = framework is difficult (D), moderate (M), or easy (E) to parameterize, run, and understand the output.
Output = difficult [D], moderate [M]), or easy [E] to define and measure.
Scale definition (Scale def) = is the framework not well-suited (NWS), moderately well-suited (MWS), or very well-suited (VWS) to examine the scales it is defined to examine.
Transparency (Trans) = is the structure of the framework difficult (D), moderate (M), or easy (E) to understand.

were moderate or easy to parameterize, run, and understand the output and 0.90 were moderate or easily transparent. With the exception of Arc-Habcap, all frameworks in Cluster 1 had sufficient documentation to clearly understand the framework (Table 3).

Cluster 2.—Cluster 2 included all frameworks (R^2 = 0.703), with the exception of CompPATS, that were components of larger landscape modeling systems (ALCES, BOREAL, EMDS, HCI, LEAM, LEEMATH, LMS, SESI, and SIMFOR; Table 3; Fig. 4). Mean dissimilarity between all 9 frameworks was 0.302 (range: 0.119–0.500), indicating that most frameworks within the cluster were similar in their characteristic abilities. All of the frameworks in Cluster 2 have received scientific credibility through publication and all but BOREAL were spatially explicit (Table 3). However, data inputs were not readily available in agency inventories for 3 of 9 (0.33) of the frameworks; species-specific models for 4 of 9 (0.44) frameworks have not been validated; each framework is moderate or difficult to parameterize, run, and understand the output; and transparency in model structure was moderate or difficult for every framework (Table 3). Documentation for 4 (0.44) frameworks was limited or marginal. None of the frameworks in Cluster 2 used population demographics, although LEAM used surrogates of population demographics (Table 3).

Cluster 3.—Cluster 3 consisted of 10 frameworks (EAM, expert systems, HABSIM, HQ, Landscape HSI, RAMAS Landscape, SNBM, spatial optimization, SPPAREA, and WHQ; Fig. 4; R^2 = 0.887). Mean dissimilarity between all frameworks within the cluster was 0.239 (range: 0.071–0.429), indicating that most frameworks within the cluster were similar in their characteristic abilities. Cluster 3 was characterized by frameworks that were generally well documented, have attained scientific credibility, used readily accessible input data, had output that is well defined and measurable, but tended to be difficult to run, parameterize and understand the output (Table 3). Half (0.50) of these frameworks emphasized population demographics or surrogates; the structure of only 2 (0.20) frameworks in Cluster 3 was easily transparent; 8 of 10 (0.80) frameworks do not have species-specific models that have been validated; 2 (0.20) frameworks (SPPAREA and WHQ) considered habitat relationships at a single spatial scale; and all frameworks, except expert systems and HABSIM, were spatially explicit. In addition, all frameworks were very well-suited to examine the scales they were designed for (Table 3).

Cluster 4.—Cluster 4 included 3 frameworks (ArcHSI, HQI, and PSE (Fig. 4), that had the lowest within-cluster variability (R^2 = 0.887) of all clusters. Mean dissimilarity between all frameworks within Cluster 4 was 0.256 (range: 0.154–0.308), further indicating that frameworks within this cluster were similar in their characteristic abilities. All of the frameworks in Cluster 4 used readily available input data, had sufficient documentation to understand the framework, and were moderately well-suited to examine the multiple scales they were designed to evaluate (Table 3). None of the frameworks in Cluster 4 used population demographics or surrogates or have been validated through species-specific models. These frameworks are mixed (difficult, moderate, and easy; Table 3) relative to our assessment of practitioners being able to measure model output and understand framework transparency.

Cluster 5.—Cluster 5 consisted of 2 spatially-explicit frameworks (BBN, HABIT@), which were both linked to the multiple scales they were very well-suited to examine (Fig. 4). Within-cluster heterogeneity was R^2 = 0.791 and within-cluster dissimilarity was 0.364. Both

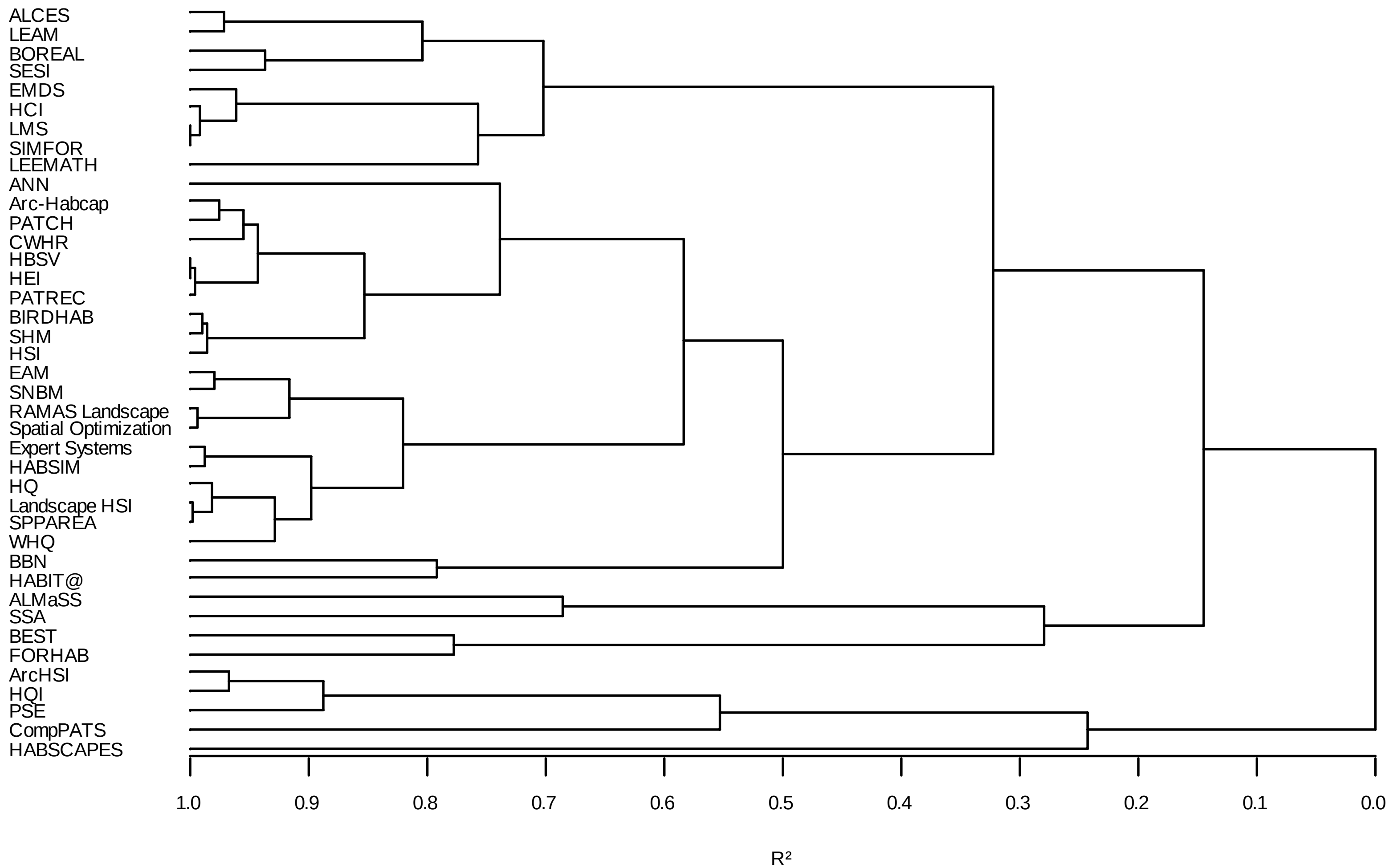

Figure 4. Hierarchical tree diagram depicting heterogeneity between clusters of 40 wildlife habitat–relationships modeling frameworks evaluated in 2007.

frameworks had sufficient documentation; were easy to parameterize, run, and provided understandable output; used surrogates of population demographics; and were ranked moderate in transparency (Table 3). BBN, but not HABIT@, attained model validation and scientific credibility (Table 3).

Cluster 6.—Cluster 6 included 2 scientifically credible, spatial frameworks (BEST and FORHAB; Fig. 4), that were moderately well suited for the multiple scales they were designed to examine (Table 3). Within-cluster heterogeneity was $R^2 = 0.778$. Dissimilarity between frameworks was 0.429, indicating that the frameworks forming this cluster were relatively more dissimilar than frameworks in the other clusters. Both frameworks incorporated surrogates of population demographics; were capable of modeling a wide range of species in a wide range of environments; but, did not have examples of validated models developed within the frameworks. However, other characteristic abilities based on rating criteria differed. BEST used readily available data from natural resource agency inventories and incorporated vegetation and its attributes within a species-habitat matrix.

Cluster 7.—Cluster 7 included 2 spatially-explicit, credible frameworks (ALMaSS and SSA; Fig. 4), which specifically relied on population demographics to evaluate wildlife–habitat relationships (Table 3). Within-cluster heterogeneity was highest in this cluster when compared among all 7 clusters ($R^2 = 0.686$) and within-cluster dissimilarity (0.400) was second highest among clusters. Input data for both frameworks were not readily available in natural resource agency inventories and neither framework has attained validation through a species-specific model. ALMaSS was suited for a single environment (i.e., temperate Europe); was moderately transparent in understanding model structure; very well–suited to examine the scales for which it was designed; was difficult to run, parameterize, and understand its output; but, has detailed documentation (Table 3). Although marginally-well documented, the structure of SSA was easily transparent, however it was rated moderate for all other ordinal-scale criteria (Table 3).

DISCUSSION

Development of model components through the last 3 decades has coincided with technological advancements including landscape modeling applications, statistical techniques, and computing capabilities (Capen 1981, Scott et al. 2002, Stauffer 2002). Developments in ecological theory have also influenced habitat–relationships modeling. For instance, some habitat–relationships modeling frameworks (e.g., HQ [Roy et al. 1995], PSE [Mead et al. 1981], WHQ [Roller 1978]) were designed to evaluate juxtaposition and interspersion of habitats based on the assumption that habitat quality is higher near edges or ecotones where wildlife are predicted to be more abundant owing to proximity of food and cover (Leopold 1933). However, edge effects are now recognized as symptomatic of habitat fragmentation and smaller patch sizes (Morrison et al. 2006); this recognition has led to a reinterpretation of edge effects for some species in habitat–relationships modeling. Newer frameworks often consider wildlife habitat relationships from a landscape viewpoint by including fragmentation or patch size effects on wildlife populations (e.g., LEAM [Aurambout et al. 2005]), grouping terrestrial species into guilds based on expected responses to different amounts and distributions of habitat across landscapes (HABSCAPES [Mellen et al. 2001]), integrating landscape and metapopulation models to predict demographic responses based on predicted landscape changes (RAMAS Landscape [Akçakaya et al. 2004, 2005]); and predicting the effects of matrix habitats, including edge responses of species, on species abundances in habitat patches (EAM [Sisk et al. 1997, Brand et al. 2006]).

Habitat suitability under HEP was defined as a 0–1 index of habitat quality ranging from unsuitable to optimal (U.S. Fish and Wildlife Service 1981). Many newer modeling frameworks (e.g., ArcHSI [Juntti and Rumble 2006], HABIT@ [McGarigal and Compton 2003], HCI [McComb et al. 2002], HQ [Roy et al. 1995], HQI [Rickel 1997], and Landscape HSI [Larson et al. 2003, 2004; Dijak et al. 2007, Rittenhouse et al. 2007]) follow this convention by defining habitat capability or suitability in 0–1 index form. This approach provides an easily interpretable basis to compare current habitat conditions or suitability of sites to optimal habitat conditions at sites for a given species.

HEP suggested that population variables should not usually be included in a habitat model because they are costly to obtain, difficult to predict, and often not indicative of habitat suitability (U.S. Fish and Wildlife Service 1981). Even though including population variables in habitat–relationships modeling may have been avoided in the past, we considered this criterion in our evaluations of modeling frameworks because the value of habitats to wildlife populations is better understood when population parameters can be linked with habitat conditions. Van Horne (1983) reported that population density by itself may be a misleading indicator of habitat quality, and that habitat quality may be more appropriately evaluated when survival and fecundity are considered along with animal densities. The results of habitat–relationships modeling are increasingly reported within a population context, including available breeding bird habitat (Smith et al. 1981), habitat effectiveness (Merrill et al. 1999), potential population density (Mattson and Merrill 2004), presence or relative abundance (Scott et al. 1993), and viable home ranges (Roloff and Haufler 1997).

Since their inception, wildlife habitat–relationships modeling frameworks have incorporated additional characteristic abilities such as application at multiple scales, linking scales when multi-scaled, and incorporation of population demographics or surrogates. Our evaluation provides practitioners with information that will be useful in selecting frameworks to meet specific needs. Below, we examine scenarios in which frameworks in each cluster have potential application. We also provide a key to assist practitioners in selecting the most appropriate framework for potential applications (Table 4).

Table 4. Key to assist practitioners in selecting the most appropriate framework for potential applications from among 40 identified wildlife habitat–relationships modeling frameworks.

1.		Large landscape modeling system is not desired ……………………...…………….	2
1.		Large landscape modeling system is desired	
	A.	Framework with scientific credibility is desired ……………..…………	Cluster 2
	B.	Framework with scientific credibility is not important ………………….	COMPATS
2.		Input data must be readily available from agency databases ……………….................	3
2.		Not critical that input data be readily available from agency databases ..……..…….	5
3.	A.	Framework where output from 1 model has been validated is desired ….....	Cluster 1
	B.	Framework where output from 1 model has not been validated is acceptable ....….	4
4.		Frameworks are very well-suited for the scales they are designed for ………...	Cluster 3
4.		Frameworks are moderately well-suited for the scales they are designed for …	Cluster 4
5.		The use of population demographics or surrogates is not an objective ….	HABSCAPES
5.		Framework which uses population demographics or surrogates is desired ……………	6
6.	A.	The spatial application of the framework simply uses geographical data ….	Cluster 6
	B	Spatially explicit applications by the framework are desired ……………….…......	7
7.	A.	Framework that uses surrogates of population demographics is desired …..	Cluster 5
	B.	Frameworks that uses population demographics is desired ………………..	Cluster 7

Potential Applications

Cluster 1.—Frameworks forming Cluster 1 provide many characteristics that practitioners may find desirable including data inputs that are readily available, field validation, scientific credibility, transparency, and the added benefit of using population demographics or surrogates to model habitat relationships. Although Cluster 1 included frameworks that evaluate wildlife habitat quality within the simplistic context of species-habitat matrices, as compared to frameworks that rely on more complex emerging analysis techniques, the characteristic abilities of frameworks using these approaches was similar. A practical application of species-habitat matrix frameworks is their use when conducting environmental impact assessments, where the quality of habitat for various species within impacted or non-impacted habitats or habitat structural stages is of more importance than predicting occurrence or abundance (Kilgo et al. 2002). Although they provide interpretable output, frameworks that use emerging analysis techniques may require technical support to parameterize and interpret model output. For instance, to model habitat relationships, ANN uses artificial neural networks (Özesmi and Özesmi 1999, Lusk et al. 2002, Özesmi et al. 2006); PATREC uses Bayesian probabilities (Williams et al. 1977, Grubb 1988); CWHR provides an option to apply fuzzy logic to calculate habitat suitability indices (California Department of Fish and Game 2005); and HBSV is a habitat-based approach to population viability modeling (Roloff and Haufler 1997, 2002). The original HSI framework provides advantages in ease of interpretability and has many completed models that have been validated. In addition, techniques are available to evaluate the reliability in HSI model inputs, providing a means to infer differences between HSI scores (Bender et al. 1996, Burgman et al. 2001). Those wishing to select a framework that uses surrogates or population demographics to link with habitat conditions should also consider Cluster 1. In comparison, frameworks in Cluster 4 do not incorporate a habitat-population linkage, and fewer frameworks in Clusters 2 and 3 provide these options as compared to Cluster 1.

Cluster 2.—Each of the modeling frameworks comprising Cluster 2 is scientifically credible components of larger landscape modeling systems. Thus, practitioners may want to consider selecting these frameworks only if they are going to be involved in a comprehensive assessment of a large landscape and therefore are willing to devote the effort necessary to parameterize and run the more comprehensive landscape model. It may be advisable for practitioners to establish a dialogue with the developers of these systems prior to initiating modeling—without establishing such dialogue, it would be difficult for practitioners to independently implement these frameworks. LEEMATH was developed to evaluate alternative management strategies for multiple species in industrial forest landscapes in the southeastern United States (Li et al. 2000); however, all other frameworks in Cluster 2 are suitable for a wide range of species in a wide range of landscapes. Major weaknesses of Cluster 2 are that only LEAM uses surrogates of population demographics, and without consultation with framework developers, transparency of the structure of frameworks is moderate at best. An advantage of several frameworks in Cluster 2 is that websites have been provided that detail their application (i.e., ALCES, EMDS, HCI [via CLAMS; Spies et al. 2002], LEAM, LMS, SESI, SIMFOR). Limitations associated with availability of input data, documentation, model parameterization, and transparency for frameworks in this cluster are largely related to the fact that these frameworks are components of larger landscape modeling systems. However, the value of understanding the influences of landscape processes and management activities such as logging on wildlife habitat quality makes consideration of these frameworks advantageous over those in other clusters.

Cluster 3.—Each framework in Cluster 3 was scientifically credible and used readily available input data, but only EAM and SNBM had models that have been field verified. Frameworks forming Cluster 3 approach habitat modeling under the context of a modeling shell (expert systems and spatial optimization), a GIS-based modeling system (Landscape HSI, RAMAS Landscape), or a modeling framework that uses a diversity of techniques to model habitat relationships. For instance, EAM utilizes a variety of spatially explicit analyses to predict the effects of matrix habitats on species abundances in habitat patches (Sisk et al. 1997, Brand et al. 2006) and SNBM generates expected distributions for wildlife species without hypothesizing spatial factors that regulate the distribution of resources or organisms (Milne et al. 1989). Spatial optimization allows one to apply the results of habitat modeling to optimize habitat configurations. However, implementation of habitat modeling with spatial optimization requires strong quantitative skills. RAMAS Landscape (Akçakaya et al. 2004, 2005) provides practitioners with a useful website and integrates a landscape model (LANDIS; He et al. 1999) with a metapopulation model (RAMAS GIS; Akçakaya 1998). Expert systems offer modelers the ability to structure models with expert opinion and quantitative data, often within the structure of a modeling shell (e.g., Sodja et al. 2002). A major advantage of frameworks in Cluster 3 compared to other clusters is the flexibility in modeling through modeling shells, GIS-based modeling systems, and other innovative techniques. A disadvantage of several frameworks in the cluster (i.e., EAM, HABSIM, HQ, SNBM, and WHQ) is marginal documentation.

Cluster 4.—Major strengths of frameworks in Cluster 4 are input data that are readily available in agency databases, abilities to evaluate spatial or spatially explicit data, and sufficient documentation to clearly understand each modeling framework. A major advantage of frameworks in Cluster 4 is their simple approach to evaluate habitat quality. ArcHSI and HQI are more sophisticated versions of the original HSI framework, are easy to parameterize and understand model output, and were developed for use within a GIS—ArcHSI was designed to work directly with ArcGIS (Juntti and Rumble 2006) and HQI with ArcView (Rickel 1997; Environmental Systems Research Institute, Inc., Redlands, California, USA). PSE uses simple landscape metrics to evaluate habitat quality with single variable data bases (Mead et al. 1981, Lyon et al. 1987). Although frameworks in Cluster 4 use simple approaches to model habitat quality, they are limited by their inability to link habitats with populations, and only PSE has achieved scientific credibility.

Cluster 5.—Cluster 5 is the only cluster where all frameworks link multiple scales. In addition, unlike the linked multi-scale frameworks in Cluster 3, HABIT@ and BBN use surrogates of population demographics in assessing wildlife habitat quality. BBN provides practitioners with endless opportunities to evaluate habitat quality through depicting probabilistic relations among variables (Marcot et al. 2001, Raphael et al. 2001, Marcot 2006). HABIT@ represents one of the most innovative frameworks because it evaluates linked, spatially explicit habitat attributes at local, home range, and population scales (McGarigal and Compton 2003).

Cluster 6.—Cluster 6 is characterized by spatial frameworks that predict changes in habitats. FORHAB predicts changes in bird breeding habitats (Smith et al. 1981), while BEST is based on a species-habitat matrix that provides predictions of where land uses may conflict with the conservation of biotic elements of the landscape (Crist et al. 2000). In addition to predictive abilities, other strengths of frameworks in Cluster 6 include scientific credibility and linkage between habitats and populations. Limitations of frameworks in Cluster 6 include limited or marginal documentation, no model validation, and models where functional transparency is marginal or difficult to understand.

Cluster 7.—Frameworks in Cluster 7 provide predictive tools that are useful in assessing impacts of land management activities on species and habitats. These predictive frameworks are stronger than those in Cluster 6 because they are spatially explicit and directly use population demographics to evaluate habitat quality. ALMaSS answers policy questions regarding effects of changing landscape or management scenario on selected wildlife species, however, it was specifically developed to model wildlife habitats in temperate Europe (Topping et al. 2003) and may have limited application elsewhere. SSA focuses on species that have the potential to be adversely affected by proposed land management due to specific habitat requirements or characteristic responses to management activities (Reed et al. 2001; Higdon et al. 2005, 2006). Weaknesses of frameworks in Cluster 7 include input data are not readily available in agency databases, models have not been validated, and frameworks are difficult or marginal to parameterize and understand the output.

FUTURE DIRECTIONS

Many recently developed modeling frameworks incorporate linkages between habitats and populations at multiple scales and link those scales, while incorporating spatially explicit data. We suggest that developers of new frameworks should consider incorporating these components because the ecological concepts addressed provide a better understanding of wildlife-habitat relationships and management implications. An emerging trend in wildlife habitat–relationships modeling is for frameworks to be components of larger landscape modeling systems. Although we view this trend as potentially problematic for practitioners not involved in comprehensive landscape assessments, many contemporary frameworks still allow independent applications.

Habitat suitability index models were originally developed to assist in quantifying and evaluating the effects of management actions on wildlife populations and their habitats (U.S. Fish and Wildlife Service 1981). Since the development of HEP, many other habitat–relationships modeling frameworks have also focused on evaluating land management actions on wildlife habitats. For instance, some frameworks have been developed to evaluate prescriptions for harvesting timber on wildlife habitats (e.g., BOREAL [Puttock et al. 1998], LEEMATH [Li et al. 2000]), whereas others consider influences of a variety of perturbations and ecological and industrial issues in conjunction with wildlife habitats (e.g., ALCES [ALCES 2005], CompPATS [Ouachita National Forest 1988], LMS [Marzluff et al. 2002], SESI [Curnutt et al. 2000], SIMFOR [Seely et al. 2004]). Future frameworks that focus on evaluations of management practices or perturbations on wildlife habitats will be more widely applied if they address a variety of management questions (e.g., energy development, transportation corridors).

A current trend in framework development is to incorporate spatially explicit procedures when evaluating wildlife–habitat relationships. We suggest that all future frameworks be developed to evaluate habitat conditions under explicit spatial contexts. Spatially explicit habitat modeling frameworks provide practitioners with the ability to evaluate habitat in relation to conditions in adjoining parcels, according to configurations of resources, and, in relation to habitat features such as roads that may influence animal movements or other behaviors (McGarigal and Compton 2003).

Emerging frameworks that show promise for describing wildlife–habitat relationships and that may be considered by developers include Petri nets, which are mathematical tools that are useful for modeling concurrent, distributed, asynchronous behavior in a system (e.g., Gronewold and Sonnenschein 1998). Also, qualitative modeling (e.g., loop analysis [Justus 2006]) may be more practical as a framework than quantitative modeling, because qualitative models require fewer resources and less modeling experience.

Developers of frameworks have consistently attained scientific credibility through published manuscripts describing the development or applications of models developed within their frameworks, but a major weakness for many frameworks continues to be a lack of validation (Raphael and Marcot 1986, Block et al. 1994, Roloff and Kernohan 1999). Model validation is critical so that models developed within any framework can be used with confidence. Therefore, we recommend that models be validated through independent field study or by reserving some data used in model development. Of particular interest is the need to validate frameworks. Although some frameworks have been validated (e.g., BIRDHAB [Kilgo et al. 2002], CWHR [Block et al. 1994], EAM [Sisk et al. 1997], SHM (Karl et al. 2000]), validation has typically been applied to individual species models developed within the structure of frameworks. Both frameworks and models need validation—a framework may work well conceptually, while a specific habitat relationships model developed within the framework may not. Although we focused on evaluating whether at least one species-specific model within a framework had been validated, we suggest that the need to validate frameworks is of even greater importance.

We suggest developers of future frameworks carefully consider the capability of practitioners to develop and apply models. Specifically, developers of new frameworks should consider using input data that are readily available in agency inventories, and develop frameworks with transparent structure and adequate documentation so that practitioners may clearly understand and apply the framework. Although we suggest that new frameworks should focus on using data from agency databases, we remind practitioners that if available data are poor quality or fail to adequately describe variables critical to the habitat requirements of a species, then only poor quality outputs will result. Thus, obtaining quality input data is paramount to producing high quality models. A particularly important consideration for new frameworks is ensuring the availability of documentation, either online or printed user's manuals that clearly describe application of models developed within the framework, present examples of model applications, offer other resources such as descriptions of input and output data, and provide schematic descriptions of framework structures to enhance understanding of the model applications by practitioners.

As model frameworks become more sophisticated, users will increasingly face the issue of parameterizing complex models for species whose ecological relationships may not be well understood. For instance, the current understanding of spatial relationships and even basic habitat associations is poor for many vertebrates (e.g., USDA Forest Service 2006). Therefore, it will be important to retain the ability within potentially complicated frameworks to develop simple models that reflect the level of ecological understanding for particular species.

ACKNOWLEDGMENTS

J. B. Haufler and G. J. Roloff provided expert reviews of our initial compilations of modeling frameworks. R. M. King, USDA Forest Service, Rocky Mountain Research Station, provided statistical assistance. J. B. Haufler, G. D. Hayward, B. G. Marcot, J. J. Millspaugh, and F. R. Thompson, III, reviewed earlier drafts of this manuscript. We thank them for their insightful reviews. Funding for our work was provided by the USDA Forest Service; Washington Office; Watershed, Fish, Wildlife, Air, and Rare Plant Staff (University of Wyoming Project Number USDAFS45321).

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