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An evaluation of New England cottontail habitat restoration

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AN EVALUATION OF NEW ENGLAND COTTONTAIL HABITAT RESTORATION

BY

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ABSTRACT

AN EVALUATION OF NEW ENGLAND COTTONTAIL HABITAT RESTORATION

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Several state, federal and non-profit agencies have developed collaborative goals for restoring habitat in New England and New York for a declining rabbit species, the New England cottontail (*Sylvilagus transitionalis*, NEC). My goal was to evaluate habitat restorations at both the local, or site, scale, and the landscape scale. In order to objectively quantify the suitability of the sites being managed, I developed a Habitat Suitability Index, based on the HSI models designed the U.S. Fish and Wildlife Service. I identified candidate habitat variables for NEC, including types of cover and refuges, and food, and then asked a panel of NEC experts to rank the importance of the candidate variables. I collected data on the most important habitat variables at 60 sites managed for NEC across New England and eastern New York. The NEC experts also ranked the same 60 sites from 1 (unsuitable) to 5 (optimal). The model was optimized to improve agreement with expert opinions for the 60 sites. Specific applications may include determining when a site is suitable for releasing translocated or captive breed rabbits, and identifying habitat features that need modification as forest succession progresses. To evaluate habitat restoration efforts at a larger landscape scale, I created metapopulation models for two management focus areas (Cape Elizabeth and Kittery-

Berwick) in Maine for population viability analyses. I ran simulations to compare the relative effects of the two focus areas as well as five management scenarios. I conducted a sensitivity analysis to determine the importance of various model parameters on extinction risk. The Cape Elizabeth focus area, which has more habitat patches that are closer together, had lower extinction risks than Kittery-Berwick. Reintroductions and creating additional habitat appeared especially important in the Kittery-Berwick focus area. The simulation results were sensitive to changes in the standard deviations of the survival and recruitment rates, and the probability of catastrophic mortality, indicating that variation is detrimental to NEC metapopulation growth. Variation in weather caused by climate change may need to be mitigated by monitoring and managing NEC habitat and populations.

CHAPTER I

INTRODUCTION

The New England cottontail (*Sylvilagus transitionalis*, NEC) is a lagomorph that occurs in southern New England and eastern New York (Chapman et al. 1992). It relies on dense shrublands and other types of early-successional habitat (Litvaitis 1993). Historically, such habitats were associated with wetlands, rock outcrops and naturally-disturbed forest patches that were a consequence of hurricanes, fires, and beaver dams (Litvaitis 2003). Beginning in the mid 1800s, abandoned farms in the region grew into shrublands and young forests (Litvaitis 2003). As a result, NEC habitat was abundant and the species was common throughout its geographic range. However, by the early 1960s, the majority of abandoned farmland matured into to closed-canopy second-growth forests that are unsuitable for NEC (Litvaitis 1993). Development and limited timber harvests have further reduced and fragmented NEC habitats (Litvaitis et al. 2006). Today, remaining NEC utilize human-altered habitats including abandoned agricultural fields, railroad corridors, and powerline rights-of-way (Litvaitis 1993).

As a result of shrinking habitat and increasingly isolated patches, NEC and other species dependent on thicket habitats have experienced substantial population declines. By 2004, NEC occupied only 14% of the historic range (Litvaitis et al. 2006). It is listed as endangered by the states of New Hampshire and Maine, is a species of conservation concern in New York and Rhode Island, and was a candidate for the federal Endangered Species List.

Currently, remnant populations are restricted to small, isolated habitat patches. Barbour and Litvaitis (1993) observed that NEC occupying habitat patches < 2.5 ha were smaller, consumed lower quality forage, and had lower survival rates than rabbits occupying larger patches. Rabbits on small patches were food limited, and thus suffered higher mortality rates because they frequently foraged away from cover where they were more vulnerable to predation (Villafuerte et al. 1997).

Although individual patch characteristics are important in determining NEC survival, landscape characteristics are also critical. Habitats near disturbed areas, with high perimeter to area ratios, and with high habitat heterogeneity are associated with lower survival rates (Brown and Litvaitis 1995). Litvaitis et al. (2003) found that the species occupied old agricultural fields in close proximity to powerlines, railroads, and highway corridors characterized by dense understory vegetation. Using Geographic Information System data, Tash and Litvaitis (2007) report similar findings throughout the current range of NEC.

Because of the contraction of the range of NEC, populations are geographically isolated from one another, raising concerns about the short and long-term viability of the NEC (Fenderson et al. 2014, Amaral et al. 2016). Remnant populations may even be further broken down into smaller metapopulations because of dispersal obstacles (e.g. multi-laned highways). At the landscape scale, the demography of each patch influences the viability of a metapopulation; for example, patches of different sizes are known to have different NEC survival rates (Barbour and Litvaitis 1993, Brown and

Litvaitis 1995). Local populations may act as “sources” or “sinks”, where sources are populations with high survival rates that produce surplus rabbits; and sinks are populations where survival and reproduction are below maintenance rates (Hanski 1998). As a result, sink patches rely on source patches for the immigration of individuals. For NEC, if the sink habitats are too numerous relative to source habitats, the metapopulations will continue to decline.

A COLLABORATIVE APPROACH

The U.S. Fish and Wildlife Service is responsible for listing endangered species. They take into consideration the current threats to the species including habitat or range contraction, diseases, over-utilization, as well as the current protection afforded by other laws, and any other factors deemed relevant. NEC was a candidate species for several years before a listing decision was made in 2015. Historically, the Service has made this decision by collecting information from states, universities, and various other sources. Once listed, regulations meant to protect the species are enacted and enforced by the Service.

In recent years, three instances of a more proactive approach to endangered species listing have occurred: the lesser prairie chicken (*Tympanuchus pallidicinctus*), sage grouse (*Centrocercus urophasianus*), and NEC. In these cases, multiple organizations have stated a common interest in conserving the species and providing information and plans to the U.S. Fish and Wildlife Service before a listing decision is made.

For NEC, a collaboration between several groups and all of the states where NEC occur has emerged (Fuller and Tur 2012). The agencies involved include the US Fish and Wildlife Service, the Natural Resources Conservation Service, state-level organizations (e.g. New Hampshire Fish and Game Department), and several non-profit agencies (e.g., the National Fish and Wildlife Foundation, Environmental Defense Fund, and Wildlife Management Institute). Products of this collaboration include a conservation strategy and reports that both guide conservation and have informed the US Fish and Wildlife Service's listing decision. As a part of the conservation strategy, the group has established goals within each state to create a total of about 21,000 ha of new habitat, including 800 ha in New Hampshire and 1,475 ha in Maine (Fuller and Tur 2012). Ultimately, the Fish and Wildlife Service's certainty that the conservation strategy would be effective was an important factor in the decision not to list NEC (U.S. Fish and Wildlife Service 2015).

Much of the habitat restoration, especially on private lands, is occurring through the "Working Lands for Wildlife" program, and other Farm Bill funded programs, provided by the Natural Resources Conservation Service (NRCS). The "Working Lands for Wildlife" program provides financial and technical assistance to private landowners in order to create or restore habitat for NEC. This program is available in the focus areas developed by each state, where habitat restoration is expected to benefit current NEC populations the most. The primary management practices used through this program are: brush management and herbaceous weed control to remove or manage invasive species and other undesirable vegetation, early-successional habitat development to remove mature trees from the canopy, and tree and shrub planting to establish native shrubs. As of 2014,over 200 habitat patches are under management, 95 of which are funded by NRCS. There is no systematic method for evaluating the success of these restoration projects, other than self-reporting from the participating organizations.

EVALUATION OF RESTORATION EFFORTS: SITE-SPECIFIC SCALE

To support a local population of NEC, a habitat patch must have certain characteristics. NEC do not migrate seasonally, and have small home ranges (Litvaitis and Jakubas 2004), so habitat patches should meet NECs needs in all seasons. Dense thickets are necessary for escape cover and are especially important for shelter in the winter. Similarly, refuges such as brush piles, abandoned burrows, and stones can provide critical protection from predators and the elements. There must be open areas with herbaceous plants to provide forage during the growing season. These habitat criteria are not captured by the current monitoring protocol (Fuller and Tur 2012).

A habitat monitoring protocol exists and is used by professionals to assess NEC habitat (Fuller and Tur 2012). While this protocol estimates dense cover based on stem density, it does not quantify other life requisites such as forage. It also does not account for the variation in cover provided by different types of stems, e.g., a rose stem tends to provide more cover than a dogwood stem. A habitat monitoring protocol should provide estimates of dense cover, forage availability, overall species composition including the status of invasives, and the spatial configuration of habitat features.

EVALUATION OF RESTORATION EFFORTS: LANDSCAPE SCALE

The viability of a NEC population depends not only on the suitability of individual patches, but the interactions amongst patches (e.g. Villafuerte and Litvaitis 1996, Fenderson et al. 2011). Therefore, an evaluation of management on a landscape-scale is necessary in determining the extent to which habitat management is aiding, or will aid, in NEC population growth and stability. Because distinct habitat patches interact with each other via the dispersal of individual rabbits, I propose examining the effects of management on a metapopulation level. While management efforts have been guided towards focus areas where NEC exist in an attempt to augment current metapopulations (Fuller and Tur 2012), it is not known how effective this strategy is, or what level of management would be required to sustain a metapopulation.

Several studies have examined the effects of habitat patch size, quality and spatial distribution on metapopulation growth of various plant and animal species (Akcakaya et al. 2004) including NEC (Villafuerte and Litvaitis 1996). Modeling is commonly used for such objectives because it provides an opportunity to conduct simulations that would not be feasible otherwise. For example, it would require immense resources and time to conduct a real experiment in which habitat availability was manipulated to determine the effects on NEC population growth.

A metapopulation model can be used for population viability analyses (PVA). Essentially, a PVA provides predictions of population growth, decline, or extinction over time based on the input parameters, including habitat availability (Akçakaya et al. 2005, Blomberg et al. 2012). A PVA includes many factors affecting the growth or decline of the species, including vital rates and stochasticity, making it more realistic than a population estimate based on habitat availability alone (Akçakaya et al. 2005).

There are several examples of metapopulation models being used to evaluate the effects of management on population viability that may have implications for NEC. Notably, Blomberg et al. (2012) modeled ruffed grouse (another declining species requiring early successional habitat) metapopulations to compare many small habitat patches to fewer large patches as management alternatives. They found that large patches resulted in a slower population decline, and recommended creating large patches rather than small patches resulting in the same total area (Blomberg et al. 2012). A study of NEC using metapopulation modeling found that environmental correlation (e.g., snow conditions are relatively uniform across the metapopulation, affecting individuals similarly) and habitat loss were important factors in the extinction risk of theoretical NEC metapopulations (Villafuerte and Litvaitis 1996).

OBJECTIVES

Currently, there is no standardized method for evaluating the suitability of NEC habitat patches that incorporates all critical habitat features. On the landscape scale, each state has proposed habitat management goals and they have implemented some portion of those goals, but have not evaluated the effects of management on NEC population viability. Considering that the U.S.Fish and Wildlife Service did not list NEC as endangered in 2015 due in part to the expected effects of on-going habitat restoration efforts, I propose the following objectives to evaluate the success of these efforts:

1. Develop a standardized NEC habitat monitoring protocol that evaluates management activities relative to habitat suitability at the site-specific scale. The protocol shall assess the abundance of critical habitat components, including security cover and forage.
2. Evaluate the effects of habitat management at the landscape scale using population viability analyses. These analyses will estimate the extinction risk of NEC metapopulations during a 15 year simulation horizon, given the amount and spatial configuration of habitat patches in different management focus areas.

ORIGINAL CONTRIBUTION BY M.S. CANDIDATE IN CHAPTER TWO

INCLUDES PARTICIPATION IN STUDY DESIGN, ALL DATA COLLECTION AND

ANALYSES, AND INITIAL DRAFT OF THE CHAPTER.

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CHAPTER II

DEVELOPING A HABITAT SUITABILITY INDEX TO GUIDE RESTORATION OF NEW ENGLAND COTTONTAIL HABITATS

INTRODUCTION

In the northeastern United States, New England cottontails (Sylvilagus transitionalis, NECs) are among the diverse taxa dependent on the dense understory vegetation of regenerating forests and native shrublands (Litvaitis et al. 1999). Historically, these habitats (collectively referred to as "thickets") were a consequence of natural (e.g., wind-blow downs, fire, riparian floods, and beaver impoundments) and anthropogenic (e.g., aboriginal fires and agriculture) disturbances or physical properties (e.g., distinct microclimates and low soil moisture) that set back or limited forest succession (Litvaitis 2003). In recent times, thicket habitats have undergone a "boom – bust cycle" largely as a consequence of widespread abandonment of farmlands, suppression of natural-disturbance regimes, and changes in land-use patterns (Litvaitis 1993).

Since the early 1970s, wildlife biologists have noted that the abundance and distribution of NECs were declining (e.g., Linkkila 1971, Johnston 1972, and Jackson 1973). In 1989, the United States Fish and Wildlife Service acknowledged that decline and included NECs as a candidate species for threatened or endangered status (USFWS 1989). A subsequent range-wide survey revealed that remaining populations were disjunct and occupied approximately 14% of their historic range (Litvaitis et al. 2006). As a result, NECs were considered for listing under the federal Endangered Species Act (Fuller and Tur 2012).

Rather than delay recovery until a listing decision is made, several governmental (United States Fish and Wildlife Service, Natural Resources Conservation Service, and state fish and wildlife agencies within the current range of NEC) and non-governmental organizations (e.g., Environmental Defense Fund, National Fish and Wildlife Foundation, National Wild Turkey Federation, Wildlife Management Institute, and local land trusts) have initiated efforts to restore and expand populations of NECs (Arbuthnot 2008, Fuller and Tur 2012). These efforts include a systematic undertaking to develop and maintain >20,000 ha of habitat for NECs on public and private lands (Fuller and Tur 2012) and were recently considered sufficient to forego listing NECs as threatened or endangered (USFWS 2015).

Although much is known about the habitat associations of NECs (Barbour and Litvaitis 1993, Brown and Litvaitis 1995, Tash and Litvaitis 2007), there is no obvious approach for evaluating the suitability of managed sites. Such a procedure could help gauge the success of overall restoration efforts and aid in developing specific recovery protocols (e.g., determine when a site is suitable for releasing captive-bred or translocated rabbits). In response to that need, we sought to develop a method that managers could use to monitor progress in generating thicket habitats and be able to determine when those habitats were suitable for NECs.

Our approach was patterned after models developed by the United States Fish and Wildlife Service (USFWS 1981). Habitat suitability index (HSI) models have been widely applied to quantify current and future habitat conditions while assessing human impacts or management alternatives (e.g., Schamberger and Krohn 1982). Essentially, HSI models generate a rating for a site from 0 (poor or unsuitable) to 1 (maximum suitability) based on measurements of species-specific habitat features or life requisites (food, cover, breeding sites, etc.). Typically, HSI models were based on literature reviews and expert opinions, with little or no validation (USFWS 1981, Brooks 1997). However, a number of studies subsequently compared HSI model output to a measure of productivity (e.g., population density or occupancy rates) of the target species (summarized by Terrell and Carpenter 1997). Results of those evaluations were mixed. Some studies found little correlation between HSI model outputs and population data, suggesting that expert-opinion models failed to identify the appropriate habitat variables or their relationships to suitability (Robel et al. 1993, Terrell and Carpenter 1997). However, using population data to verify model performance can be problematic. Animals may move into an area of low overall habitat quality for a variety of reasons (e.g., response to territoriality or social hierarchy) and similarly, animals may be missing from high-quality sites as a consequence of exploitation or density-independent factors, thus reducing the utility of population density and occupancy as indicators of habitat suitability (van Horne 1983, Burgman et al. 2001). Survival rates or fecundity may be more appropriate surrogates for carrying capacity (van Horne 1983); yet those parameters are infrequently used (Roloff and Kernohan 1999).

Among other studies, however, expert-opinion models performed similarly to empirical models (Bowman and Robitaille 2005, Germaine et al. 2014). Additionally, expert-opinion models can be optimized with field data to improve their predictive power (Cook and Irwin 1985, McComb et al. 1990, Terrell and Carpenter 1997).

Our goal was to develop a HSI-based model that could be used to evaluate parcels of land that have been included in the multi-state NEC restoration effort. We envisioned that our protocol would have several distinct, site-specific applications. First, it could provide a consistent approach for monitoring management actions and help identify potential limitations of a site prior to releasing cottontails. Such an approach could also be used to prioritize actions among multiple sites or rank suitability of them. Finally, an HSI model could be used to track suitability of one site over time and alert managers to specific features that may need remediation (e.g., help in developing a mowing schedule). Therefore, the objectives of our study were to: i.) use literature reviews and expert opinions to identify variables that describe life requisites of NECs, ii.) develop suitability indices for those variables that can be incorporated in a simple model to rank specific sites, and iii.) optimize the resulting model using information on NEC occupancy and expert rankings of surveyed sites.

STUDY AREAS

We restricted our field efforts to managed sites within the occupied range of NECs (Litvaitis et al. 2006) that were contained in management focus areas described in the NEC conservation strategy (Fuller and Tur 2012). This region is in the northeastern United States, from the Hudson River Valley in New York, portions of Connecticut, Massachusetts, Rhode Island, southeastern New Hampshire, and southwestern Maine (Fig. 1). In southern areas and along the Atlantic coast, forests are dominated by oaks (Quercus spp.) and pines (Pinus spp.). To the north, forest types include maples (Acer spp.), birches (Betula spp.), and American beech (Fagus grandifolia). Land uses vary throughout the region. In general, southern and coastal areas are characterized by a mix of urban/suburban developments, small woodlots, and scattered agricultural fields. Inland landscapes are dominated by large blocks of mid-successional forests (Tash and Litvaitis 2007).

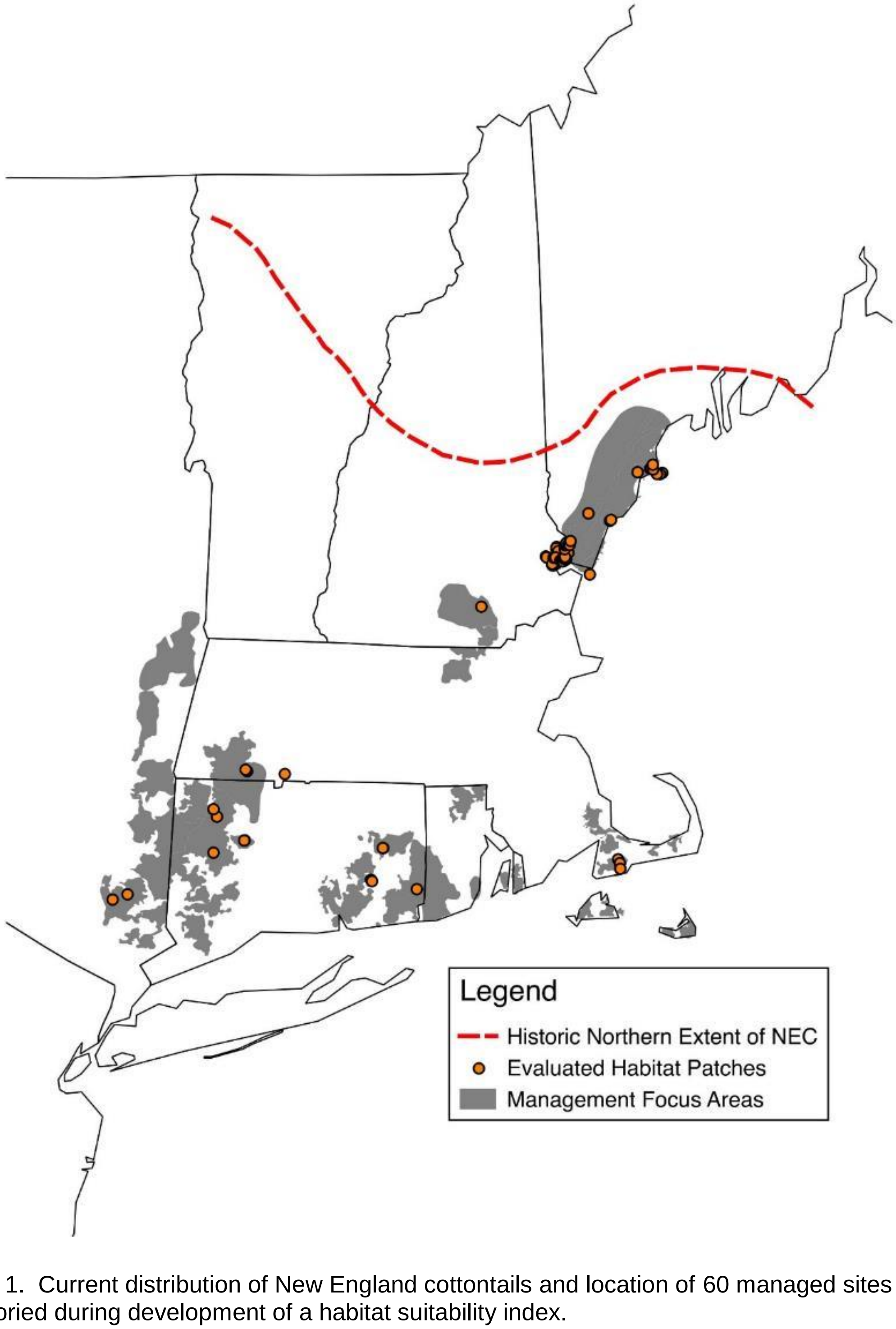

Figure 1. Current distribution of New England cottontails and location of 60 managed sites that were inventoried during development of a habitat suitability index.

MATERIALS AND METHODS

Identifying Habitat Variables

Once established on a site, NECs do not migrate or frequently move to new sites (Barbour and Litvaitis 1993), so a habitat patch must provide the resources required year round. Food and cover are patch-specific features and based on our knowledge of life requisites and published literature, we identified 10 candidate variables to describe these (Table 1). Several additional features are known or suspected to affect persistence of NEC at a local scale but were not included in our model, specifically size of habitat patch, surrounding landscape composition, proximity to other patches of habitat occupied by NECs, and presence of eastern cottontails (S. floridanus). Small patches of habitat (<3 ha) are known to function as demographic sinks for NECs (Barbour and Litvaitis 1993). As a result, Fuller and Tur (2012) did not recommend managing small parcels as part of the recovery strategy and we do not recommend application of our HSI-based approach among patches <3 ha. Landscape composition (Brown and Litvaitis 1995, Tash and Litvaitis 2006, Fenderson et al. 2014) and proximity to other parcels occupied by NECs (Litvaitis and Villafuerte 1996) may also affect local persistence of NECs. Finally, competition between NECs and expanding populations of eastern cottontails is suspected of contributing to the decline of NEC populations in some regions (Probert and Litvaitis 1996, Litvaitis et al. 2007). As a result, eastern cottontails may hinder restoration efforts. We believe that all of these features should be considered while identifying parcels for inclusion in restoration efforts, but decided not to include them in our suitability model because of obvious limitations in easily modifying them.

Table 1. Candidate variables of New England cottontail habitat based on literature review and majority opinion of their importance (ranked 1 to 4, 1 being the very important, 4 being not important) by a panel of biologists familiar with New England cottontails. Understory vegetation refers to woody vegetation with a diameter at breast height (dbh) of <7.5 cm.

Variable	**Description**	**Supporting Literature**	**Majority Opinion of Importance**
C_1: Security cover	Abundance of very dense understory vegetation that provides protection from predators and weather extremes.	Barbour and Litvaitis 1993, Brown and Litvaitis 1995, Chapman and Litvaitis 2003	1
C_2: Winter forage and escape cover	Abundance of moderately dense understory vegetation that provides cover and forage.	Dalke and Sime 1941, Barbour and Litvaitis 1993	1
C_3: Winter forage and travel cover	Abundance of less dense understory vegetation that provides cover and forage.	Dalke and Sime 1941	4
C_4: Winter forage	Availability of edible twigs, buds, leaves in winter.	Dalke and Sime 1941, Smith and Litvaitis 2000	2
C_5: Additional refuges	Presence of natural and artificial burrows, stone walls, and other structural refuges that provide protection.	Chapman 1975	2
C_6: Vegetation height	Understory vegetation of a certain height provides escape cover from aerial and terrestrial predators.	Litvaitis and Jakubas 2004, Arbuthnot 2008	1
C_7: Herbaceous forage	Abundance of grasses and forbs that provide forage during the growing season.	Dalke and Sime 1941, Smith and Litvaitis 2000	2
C_8: Summer interspersion index	Availability of forage near protective cover in summer.	Smith and Litvaitis 2000	2
C_9: Winter interspersion index	Availability of forage near protective cover in winter.	Brown and Litvaitis 1995	2
C_{10}: Coverage by invasive shrubs	Concern that invasive shrubs may not provide adequate winter food or cover.	Litvaitis et al. 2003	3

Next, 9 biologists with first-hand experience with NEC habitat were asked to review our list of candidate variables and rank their relative importance. Ranking options were: 1 (very important), 2 (moderately important), 3 (somewhat important), 4 (not important), or “I don’t know.” The implications of invasive shrubs as a detrimental feature generated inconsistent responses from the panel. Although there was some recognition that the spread of invasive plants may have negative consequences, it was also acknowledged that some invasive shrubs provide suitable cover. As a result, we eliminated this candidate variable from consideration. Rankings were then used to identify the variables that were combined or modified to facilitate measurement and subsequent incorporation into an HSI model (Table 2).

Table 2. Final group of variables selected to generate a habitat-suitability index for habitats managed for New England cottontails. Understory vegetation refers to woody vegetation with a diameter at breast height (dbh) of <7.5 cm.

Variable	Definition	Suggested Inventory Method
V1: Security cover	Percentage of the understory vegetation that has a density of >300,000 stem- cover units/ha. Includes C1+4 in Table 1.	Record understory-stem density by species in 10 x 1-m plots and convert to stem-cover units (see text for details). Placement and number of sampling plots will be dependent on the distribution of understory stems (e.g., relatively uniform woody cover = systematic distribution of plots) and size of managed site. For example, at least 2 plots/ha for large sites (>10 ha), 3/ha for medium-sized sites (5-10 ha), and 5/ha for small sites (<5 ha). Calculate the percentage of the site that contains >300,000 stem-cover units/ha.
V2: Other cover	Percentage of the understory vegetation that has a density of 100,000-300,000 stem-cover units/ha. Includes C2+3+4 in Table 1.	Inventory similar to security cover. Calculate the percentage of the site that contains 100,000-300,000 stem-cover units/ha.
V3: Height of woody cover	Average height of the understory vegetation in the patch (meters). Includes C6 in Table 1.	Measure height (m) of dominant understory vegetation in sample plots and calculate an average for the site.
V4: Summer forage	Edge-to-area ratio of herbaceous openings to woody cover (m/ha). Includes C7+8 in Table 1.	Use high-resolution aerial photography (e.g., Google Earth) to delineate the edge between woody understory cover and grass/forb openings no smaller than 3 m in diameter and determine length of edge (meters). Divide edge by area of managed site (ha). Verify the accuracy of the aerial photography in the field.
V5: Additional refuges	Presence/absence of constructed brush piles, natural or artificial burrows, rock walls, and stone foundations. Includes C5 in Table 1.	Suitable refuges noted as observed in the field.

Developing Suitability Indices

We sampled 60 sites being managed for NECs to collect information on each habitat variable (Fig. 1). These sites were located in five of the six states participating in the recovery initiative, spanned a range of restoration conditions, and included various plant communities that were under a variety of management prescriptions. Selected sites also had dominant woody vegetation that was >0.5 m tall because we considered that to be the minimum condition for NEC occupancy. At each site, we used 10 x 1-m plots to inventory the woody understory vegetation (<7.5 cm dbh), including stem density by species and dominant understory height (Table 2). The presence of potential refuges (e.g., natural or artificial burrows, intentionally-constructed brush piles, rock walls, or stone foundations) was also noted.

To adequately represent cover or visual obstruction by vegetation, we converted estimates of stem density to stem-cover units because of large differences in the amount of cover provided by different plants. To accomplish this, we estimated the cover provided by specific plants using a profile board (Nudds 1977) during leaf-off season and then applied linear regression to calculate the relative cover value of an individual stem (similar to procedures used by Litvaitis et al. 1985). For example, raspberry stems (Rubus spp.) were found to provide the least amount of visual obstruction and were assigned a stem-cover value of 1. Dogwoods (Cornus spp.) provided 4.28 times the amount of visual obstruction of raspberry stems, whereas barberry (Berberis spp.) stems provided 8.72 times more visual obstruction (Appendix A). Using that information, a hypothetical habitat patch with an average stem density of 40,000 dogwood stems/ha would have 171,200 stem-cover units/ha. The patch would have 348,800 stem-cover units/ha if all stems were barberry, but only 40,000 stem-cover units if all stems were raspberries. In previously prepared management guidelines (Arbuthnot 2008), 40,000-50,000 stems/ha was recommended as security cover for NECs. Using stem-cover units, we modified thresholds for security cover (V1) as the proportion of the patch with >300,000 stem-cover units/ha and other cover (V2) as the proportion of the patch with 100,000-300,000 stem-cover units/ha.

Ideal NEC habitat also includes openings dominated by grasses and forbs in close proximity to woody cover (Arbuthnot 2008) because cottontails do not stray far from cover to search for food (Smith and Litvaitis 2000). To describe that feature, we used an edge-to-area ratio rather than the percentage of the patch that was dominated by herbaceous vegetation. Recent aerial photographs (e.g., Google Earth) were used to measure the length of grass/forb-shrub edges and the total patch area (V4, Fig. 2).

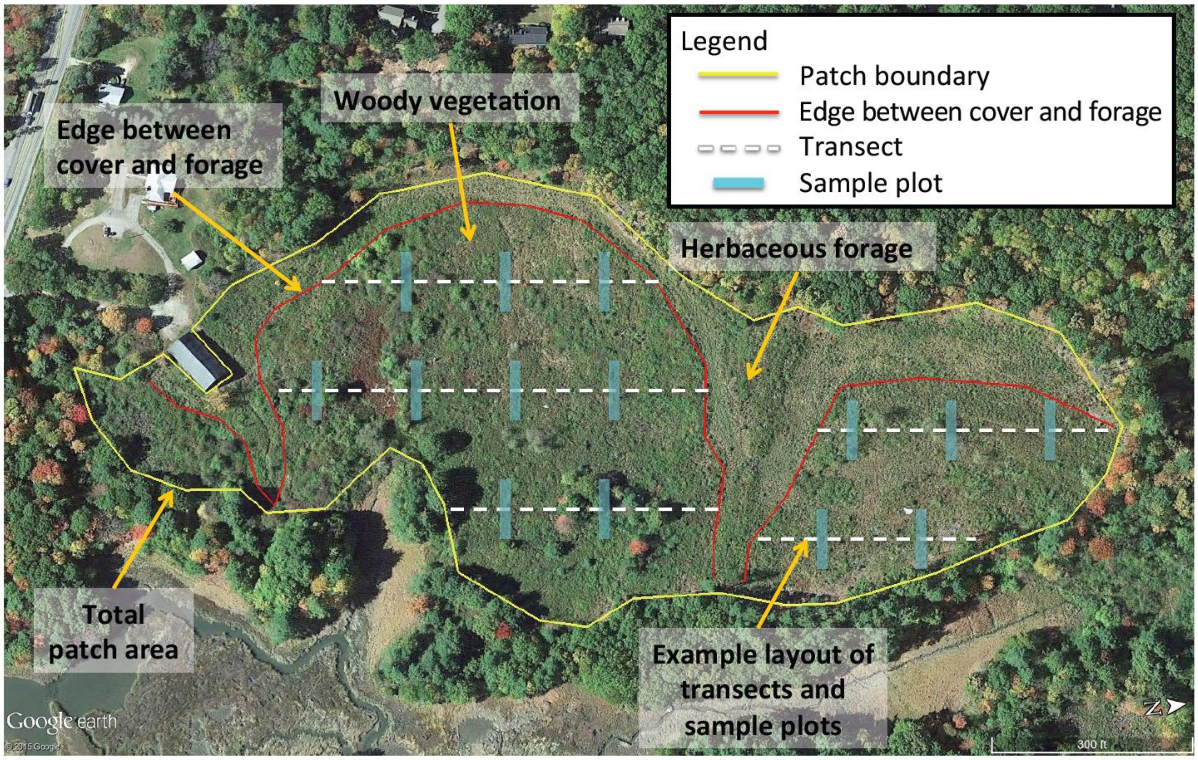

Figure 2. Aerial photograph (from Google Earth) used to measure patch area and summer forage availability (edge-to-area ratio of woody cover and herbaceous forage). Also shown is an example of the sample plot layout for assessing habitat variables 1-3 used in the habitat suitability model.

To develop suitability indices for each variable, we used an iterative process that incorporated expert opinions and field inventories. Our intent was to clearly distinguish different levels of suitability among patches. First, we asked experts to rank the 60 managed patches that we had inventoried on a scale of 1 to 5, where 1 indicated that the site was unsuitable and would require substantial management to become suitable and 5 was an ideal site that would or did support a high density of NECs. Experts were reminded to only consider patch-specific suitability and disregard surrounding landscape features that might affect dispersal/colonization by NECs. Next, we compared the habitat variables at each of these sites to the expert ranks (Fig. 3) to generate upper and lower values for suitability curves of each habitat variable. For example, we found that sites ranked as suitable or highly suitable by experts had much greater coverage of dense understory vegetation (usually >25% of patch) than sites that were ranked as marginal or not suitable (usually <5% coverage in dense understory vegetation). For our initial suitability curve of that habitat variable, index values were set a 0 (not suitable) if dense understory coverage was <5% and 1.0 (optimal suitability) if coverage was >25%. We assumed a linear increase in suitability as dense understory coverage increased from 5% to 25%. We repeated this for all variables. As model development progressed, suitability curves were modified if those changes improved our ability to separate patches into categories of suitability based on expert ranks.

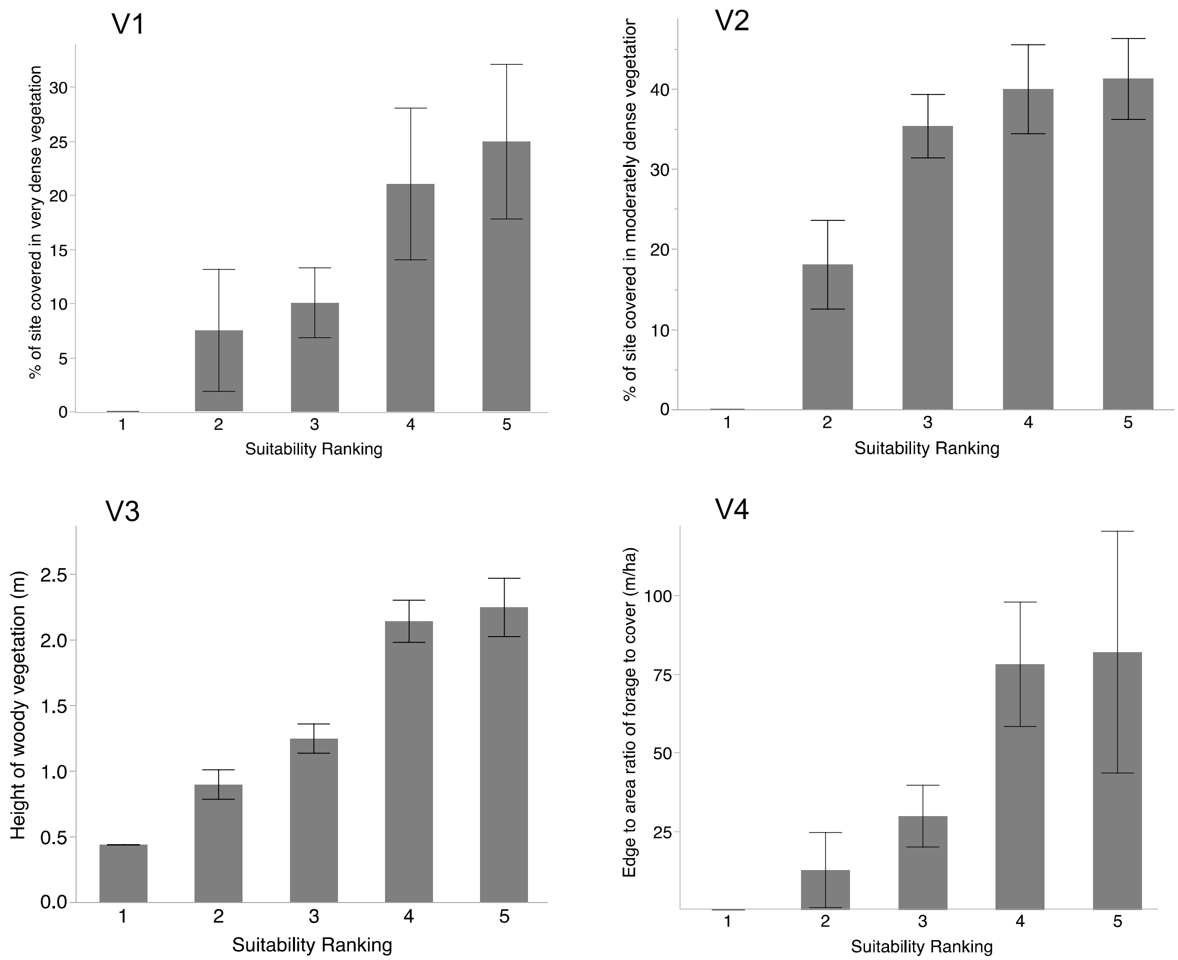

Figure 3. Average (and standard errors) values of four habitat variables sampled among 60 sites managed for New England cottontails that were also were ranked from 1 (not suitable) to 5 (highly suitable) by biologists knowledgeable on the requirements of New England cottontails.

Incorporating refuges (V5) into the HSI model presented a particular challenge. Refuges were considered a positive component of NEC habitat by the expert panel and creation of brush piles or artificial burrows was included in the management of some sites. For that reason, some sites that had limited regenerating woody vegetation (because of recent cutting or mowing) had an abundance of refuges. On the other hand, sites with substantial dense understory vegetation often lacked refuges or refuges were difficult to detect.

Optimizing the Model

Following the United States Fish and Wildlife Service protocol for developing a HSI model (USFWS 1981), individual suitability indices were combined into a function that produced a value of 0 to 1 for a site. Structuring that function required determining the relative importance (or weight) of each variable. Typically, the structure of the model is either a weighted average of the variables, or in a case where one or several variables are very influential to the survival of the species, the lowest score of those critical variables is taken as the overall suitability score (USFWS 1981).

Our literature review and expert opinions (Table 1) indicated that all five variables (Table 2) have some degree of importance to NECs; therefore, we developed a model based on a weighted average. To determine the relative contribution of each variable, we examined relationships between variable measurements, expert rankings of surveyed sites, and NEC occupancy of surveyed sites, as well as expert opinions about the importance of each variable and literature. Variables were given a higher weight if expert opinion, literature reviews, and field data were in agreement that the variable was very influential in determining habitat suitability. Variables thought to be less important by experts or indicated by field data were given a lower weight.

RESULTS

Habitat Variables and Suitability Indices

Using expert opinions and relationships between habitat variables and ranked suitability (Fig. 3), we created suitability index curves for individual variables except refuges (Fig. 4). To incorporate refuges, we simply added 0.1 to the score if refuges were found on a site or 0 if refuges were not detected (see below). The function of added refuges is to compensate for insufficient cover on the site. As a result, the suitability of a site can be enhanced with the addition of refuges but not lowered if refuges were not found, and the score cannot exceed 1.0 because that would inflate the final HSI score.

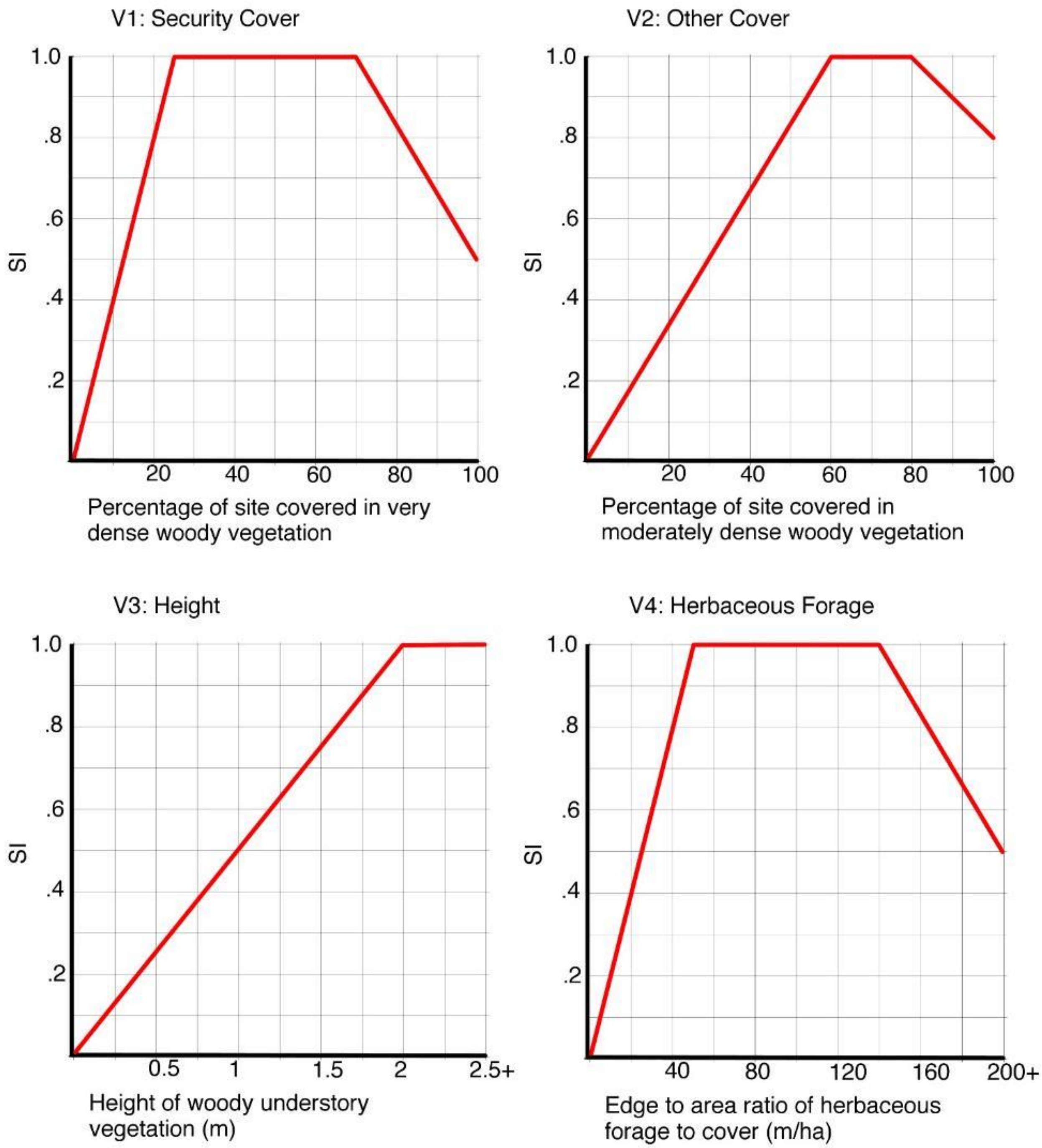

Figure 4. Suitability index (SI) curves for four habitat variables that describe life requisites of New England cottontails.

Optimized Model Structure

The final HSI model was a weighted average of four habitat variables plus the presence/absence of refuges (Eq. 1). Experts stressed the importance of dense vegetation (security cover) and previous studies showed that NECs prefer dense

$$HSI = \frac{(3 \times V1) + (2 \times V2) + V3 + V4 + V5}{7}$$

Where:

V1 = Security cover
V2 = Other cover
V3 = Vegetation height
V4 = Summer forage
V5 = Refuges (addition of V5 cannot result in the HSI exceeding 1.0)

(Equation 1)

vegetation (e.g., Barbour and Litvaitis 1993, Smith and Litvaitis 2000). That pattern was corroborated by our inventory of managed sites where those that were ranked high or were occupied by NECs tended to have a larger proportion of the site covered in dense vegetation (Fig. 3). As a result, we gave this variable (V1) a weight of 3 and other cover (V2) a weight of 2. Height of woody vegetation (V3), summer forage (V4), and presence/absence of refuges (V5) were consider as less crucial based on observed winter-mortality patterns (Barbour and Litvaitis 1993).

HSI Scores versus Expert Opinion Ranks

There was a clear relationship between the expert-opinion ranks of managed sites and the HSI generated by our model (Fig. 5). Variability in the HSI score within each expert opinion ranking category was expected. NECs could find a variety of conditions tolerable and our field measurements may not have accurately captured nuances among variables. Also, there was likely some degree of subjectivity by experts when ranking sites. Despite those difficulties, it was clear that the resulting HSI model differentiated among unsuitable (rank = 1-2), marginal (rank = 3) and suitable sites (rank = 4-5).

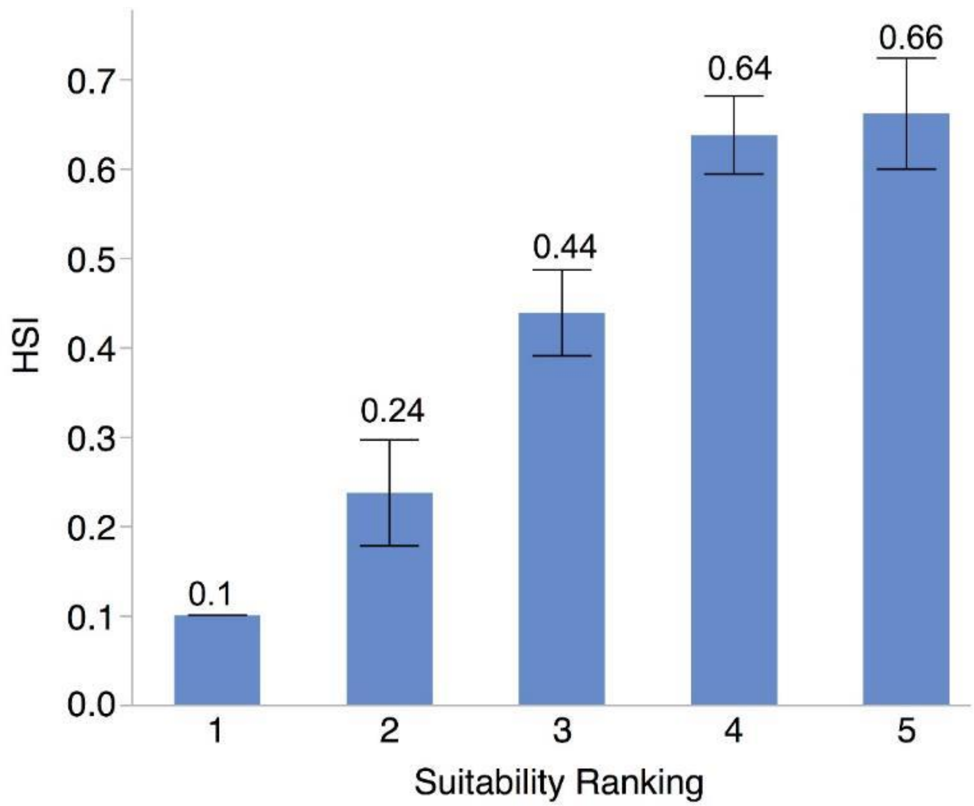

Figure 5. Average habitat suitability index model scores (and standard errors) for 60 sites with expert-opinion rankings, where 1 was assigned to the least suitable sites and 5 was assigned to the most suitable sites.

Among the 60 managed sites we inventoried, HSI model scores ranged from near 0 to 1.0 (Fig. 6). The average HSI score for the most suitable sites, as rated by the experts, was 0.66 and the average model score for NEC-occupied sites was higher (μ = 0.67, SE = 0.05) than for unoccupied sites (μ = 0.42, SE = 0.25). Therefore, an initial threshold value for releasing rabbits on an unoccupied site could be an HSI score of 0.65-0.7.

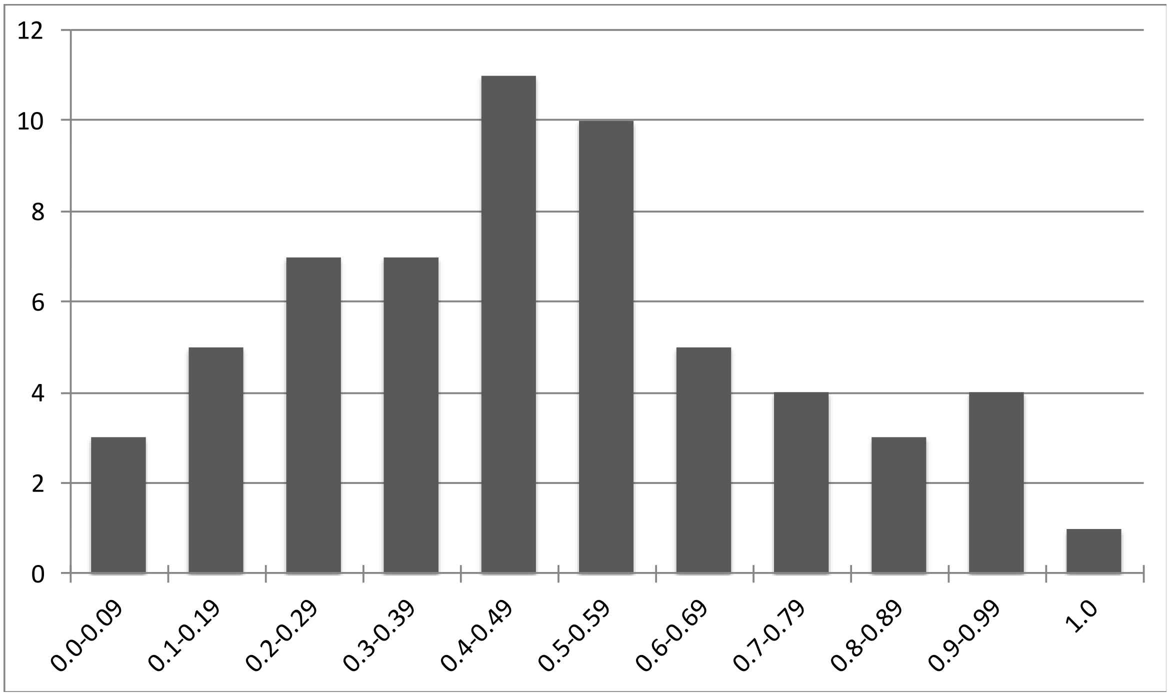

Figure 6. The distribution of habitat suitability index model scores for 60 sites managed for New England cottontails.

DISCUSSION

We believe our HSI model can facilitate restoration of NEC populations by consistently evaluating sites and identifying specific habitat components that need to be improved. Consider a hypothetical site with the following characteristics: V1 = 15% coverage (SI = 0.58), V2 = 35% coverage (SI = 0.58), V3 = 1.25 m (SI = 0.63), V4 = 38 m/ha (SI = 0.75), and V5 = Absent. Entered into our model, we generated a score just below the recommended threshold.

$$\frac{(3 \times 0.58) + (2 \times 0.58) + 0.63 + 0.75 + 0}{7} = 0.61$$

We could add brush piles or artificial burrows (we recommend 2-3/ha) to improve current conditions (HSI increases to 0.71), or wait several years until the average height of understory vegetation increases to 2 m (HSI increases to 0.66), or use both approaches (HSI increases to 0.76). On the other hand, we could expand coverage of very dense (V1) and moderately dense (V2) understory vegetation to substantially increase suitability.

Describing the suitability of a site can also be an effective approach in recruiting and retaining private landowners as partners in the restoration effort. More than half of forestland in New England is privately owned (Butler and Ma 2011), making landowner recruitment an essential component of the NEC conservation strategy. The HSI model can help in educating landowners about the needs of NECs and the management options available. It can also give participating landowners a target or management goal to achieve. Additionally, application of the HSI model can provide a structured approach for obtaining funds from such cost-share programs as the Environmental Quality Incentives Program coordinated by Natural Resources Conservation Service where limited funds could be directed toward the lands with the greatest management potential.

Although we dropped the prevalence of invasive shrubs from consideration as a habitat feature, that characteristic should not be overlooked when developing management recommendations for a specific site. We acknowledge that generically, invasive shrubs cannot be easily categorized as either detrimental or beneficial to NECs. Available information suggests that the cover value of certain invasive shrubs can be comparable or even greater than some native shrubs (Litvaitis et al. 2013) and relative value of invasive and native shrubs as winter forage are largely unknown. Additional considerations when addressing management protocols toward invasive shrubs would be their prevalence in the surrounding landscape (Litvaitis et al. 2013) and the importance of the site to other thicket-affiliated taxa. For example, some invasive shrubs support fewer insects that are an important food source of nesting songbirds and their developing offspring (Fickenscher et al. 2014). Under such conditions it would be important to consider the needs of both nesting songbirds and NECs while developing management prescriptions (Litvaitis et al. 2013).

In addition to describing applications of the HSI model, it is also relevant to describe applications that we do not believe our model should be used for. We do not believe that the evaluation of a site should be used to predict the occurrence of NECs. Landscape composition and proximity to other sites occupied by NECs are important considerations in such an evaluation and are not included in the HSI model.

Finally, an important aspect of the HSI approach is its adaptability. With new information on NEC habitat associations, our model can be updated, especially among different plant communities that were not well represented in the 60 sites we inventoried, including pitch pine-scrub oak (Pinus rigida-Quercus ilicifolia) or mountain laurel (Kalmia latifolia) dominated habitats. Releases of captive-bred and translocated rabbits to vacant habitats and subsequent monitoring of their fate should also provide opportunities to reconsider the relative weights given to variables in the HSI model.

Acknowledgments

We thank the many students and colleagues who assisted with collecting field data and locating managed habitat sites, and K. Boland, H. Holman, W. Jakubas, A.

Johnson, D. Keirstead, H. Kilpatrick, P. Novak, J. Oehler and D. Scarpitti for serving as expert-panel members. We also thank private landowners that granted us access while inventorying managed habitats. Funding was provided by the Conservation Effects Assessment Project and Working Lands for Wildlife Initiative of the Natural Resources Conservation Service and the College of Life Sciences and Agriculture at the University of New Hampshire. K. Boland, H. Kilpatrick, J. Norment, and J. Oehler provided insightful comments on early drafts of this report.

Appendix A. Relative cover values (visual obstruction) provided by selected understory shrubs and young trees encountered on managed New England cottontail habitats.

Group	Cover Value
Eleagnus	13.16
Berberis	8.72
Cornus	4.28
Young evergreen trees	65.88
Lonicera	31.09
Juniperus	14.07
Low-growing shrubs	2.63
Rubus	1.00
Rosa	5.81
Spirea	1.88
Young deciduous trees	2.65
Upright shrubs	6.56

CHAPTER III

ASSESSING NEW ENGLAND COTTONTAIL HABITAT MANAGEMENT AT A LANDSCAPE SCALE

INTRODUCTION

In response to the rangewide decline of New England cottontails (*Sylvilagus transitionalis* - NEC), several governmental (U.S. Fish and Wildlife Service, Natural Resources Conservation Service, and state fish and wildlife agencies within the current range of the New England cottontails) and nongovernmental organizations (e.g., Environmental Defense Fund, National Fish and Wildlife Foundation, National Wild Turkey Federation, Wildlife Management Institute, and local land trusts) are working in collaboration to create more habitat for this species (Fuller and Tur 2012). The management of habitat for NEC involves creating and maintaining patches of early-successional forests or shrubland habitats (Arbuthnot 2008). Restoration efforts are concentrated in focus areas to expand existing populations of NEC (Fuller and Tur 2012). For example, although NEC once occurred across much of southern Vermont and New Hampshire, and along the coast of Maine to Portland, habitat management is only occurring only in a few focus areas where NEC still occur (Fig. 7).

Habitat restoration goals have been set forth for each focus area, but it is not known how much habitat is needed to maintain stable metapopulations of NEC. Because it takes several years for most sites to become suitable after management, and NEC populations can decline for reasons other than habitat suitability, it is impractical to empirically measure the effects of habitat management on NEC abundance to refine habitat goals at this time. Under such circumstances when field experiments are not feasible due to restrictions of time, space, and cost, population viability analyses (PVA) and metapopulation simulations can be used to explore different management scenarios.

A metapopulation is a set of local populations that interact with one another via the dispersal of individuals. In recent years, NEC have been relegated to genetically and spatially distinct metapopulations (Fenderson et. al 2014). Management focus areas are intended to function as metapopulations where source and sink populations determine their viability (Fig. 8). A source population has high survival rates from which individuals frequently disperse to other populations. Sink populations, on the other hand, have low survival rates and rely on immigrants from source populations to remain occupied (Hanski 1998). The source-sink concept is particularly relevant to NEC because small habitat patches have been found to have lower survival rates (Barbour and Litvaitis 1993) and some of the metapopulations are declining because they are largely comprised of small patches (Litvaitis et al. 2006). Previous investigations of various plants and animals have examined the effects of habitat-patch size, quality, and spatial distribution of individual populations on metapopulation growth (Akcakaya et al. 2004).

Figure 7. The approximate historic northern extent of New England cottontails in northern New England, and the current management focus areas (redrawn from Fuller and Tur 2012).

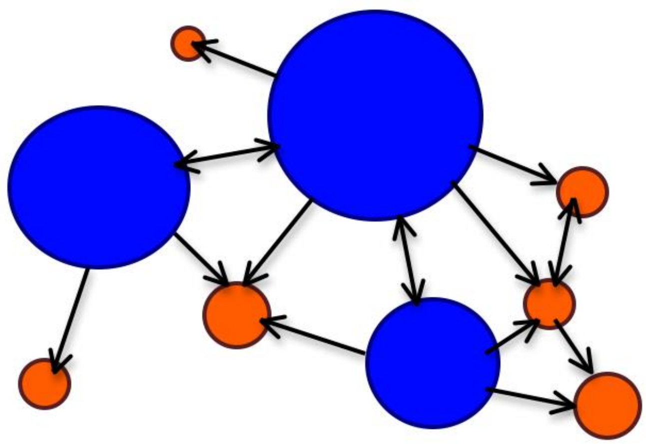

Figure 8. Illustrated metapopulation composed of source patches (blue) and sink patches (orange), where the size of the circle represents carrying capacity. Source patches supply dispersing individuals that colonize sink patches, which are vulnerable to population decline and extinction.

A metapopulation model can be constructed to run simulations and conduct PVA. A method commonly used in conservation biology is creating a model using a spatially explicit software program to estimate extinction risk, population trajectory, and other outcomes for specific management alternatives (Akçakaya et al. 2004, Blomberg et al. 2012). There are several examples of metapopulation models used to evaluate the effects of management on population viability that have implications for NEC. Notably efforts by Blomberg et al. (2012) that simulated responses by ruffed grouse (*Bonasa umbellus*) populations in response to different habitat-management strategies and found that fewer but larger patches resulted in a slower population decline. Modelling a hypothetic NEC metapopulation, Litvaitis and Villafuerte (1996) found that environmental correlation (e.g., snow conditions that are relatively uniform across a metapopulation affect individuals similarly) and habitat loss were important factors determining short-term extinction risk. Viability of a NEC metapopulation depended on the suitability of individual patches and the interactions among patches (Litvaitis and Villafuerte 1996).

Methods of modelling metapopulations and predicting extinction risk have changed rapidly alongside the advances in computing power that allows us to perform these simulations. The term “metapopulation” was introduced in 1969 (Levins), although aspects of metapopulation theory had been developed before then. Various strategies for simulating metapopulations have been developed. An important advancement was the inclusion of variability, or stochasticity, in models to better represent the uncertainty of real metapopulation dynamics. Boyce (1977) discovered that introducing stochasticity reduces the expected growth rate of the metapopulation, when compared to deterministic models using the same vital rates but no variation in the rates. This phenomenon has been found to occur in real life; environmental variation reduces population growth rates (Pickett et al. 2015). This suggests that deterministic models may underestimate minimum population sizes and minimum amounts of habitat needed for a metapopulation to persist, and underscores the importance of stochasticity for accurate modelling results.

A metapopulation model and PVA can be used to simulate habitat management activities and their effects on NEC metapopulation viability. The relative extinction risks and projected abundance of individuals can be compared between different management scenarios of interest. In the case of NEC, I am interested in evaluating the effectiveness of the focus area strategy (creating more habitat patches near other patches), as well as the role of more intensive management over time, such as maintaining the suitability of all patches that have been created and reintroducing NEC to vacant patches.

GOALS

Create a stochastic metapopulation model for NEC in two focus areas, develop various management scenarios to simulate, and compare outcomes. My goal was to inform management decisions regarding NEC habitat. My objectives were to:

1. Compare outcomes of habitat management scenarios using NEC metapopulation models for two focus areas.
2. Develop management recommendations based on NEC metapopulation simulations.
3. Identify areas for future research to improve NEC metapopulation simulations.

METHODS

Study Areas

I modeled the Cape Elizabeth, Maine and Kittery-Berwick, Maine (Fig. 9) focus areas because there have been extensive surveys of NEC populations and habitats in those landscapes (Litvaitis et al. 2003, Fenderson et al. 2014).

Both areas are in eastern temperate forest, with climate and vegetation influenced by the Atlantic coast. The Cape Elizabeth focus area is coastal, contains a number of state parks and open areas as well as residential neighborhoods. It covers two towns, Scarborough and Cape Elizabeth, and totals about 15,000 hectares, of which 262 ha are suitable (managed and unmanaged) for NEC (Table 3). The Kittery-Berwick focus area is actually two adjacent management focus areas, Kittery and Eliot-Berwick, and it includes inland and coastal areas, is more heavily forested, and covers 35,000 hectares, including 121 ha of suitable habitat (Table 3).

NEC habitat patches (Fig. 10) vary in vegetation composition, but are often dominated by native shrubs and early-successional trees (e.g. *Cornus spp., Alnus spp., Aronia melanocarpa, Kalmia latifolia, Betula spp., Pinus strobus, Prunus virginiana*), invasive shrubs (e.g., *Rosa multiflora, Elaeagnus umbellate, Lonicera spp., Berberis thunbergii*), and grasses and forbs. Many areas have wetland or coastal marshes. Most managed and unmanaged patches are former agricultural lands or areas of low quality timber that have been clearcut. Some are remote, and others are adjacent to residential or industrial areas and roads.

Figure 9: The locations of the two NEC management focus areas for which metapopulation models were developed. Both are located in Maine, in the northeastern United States.

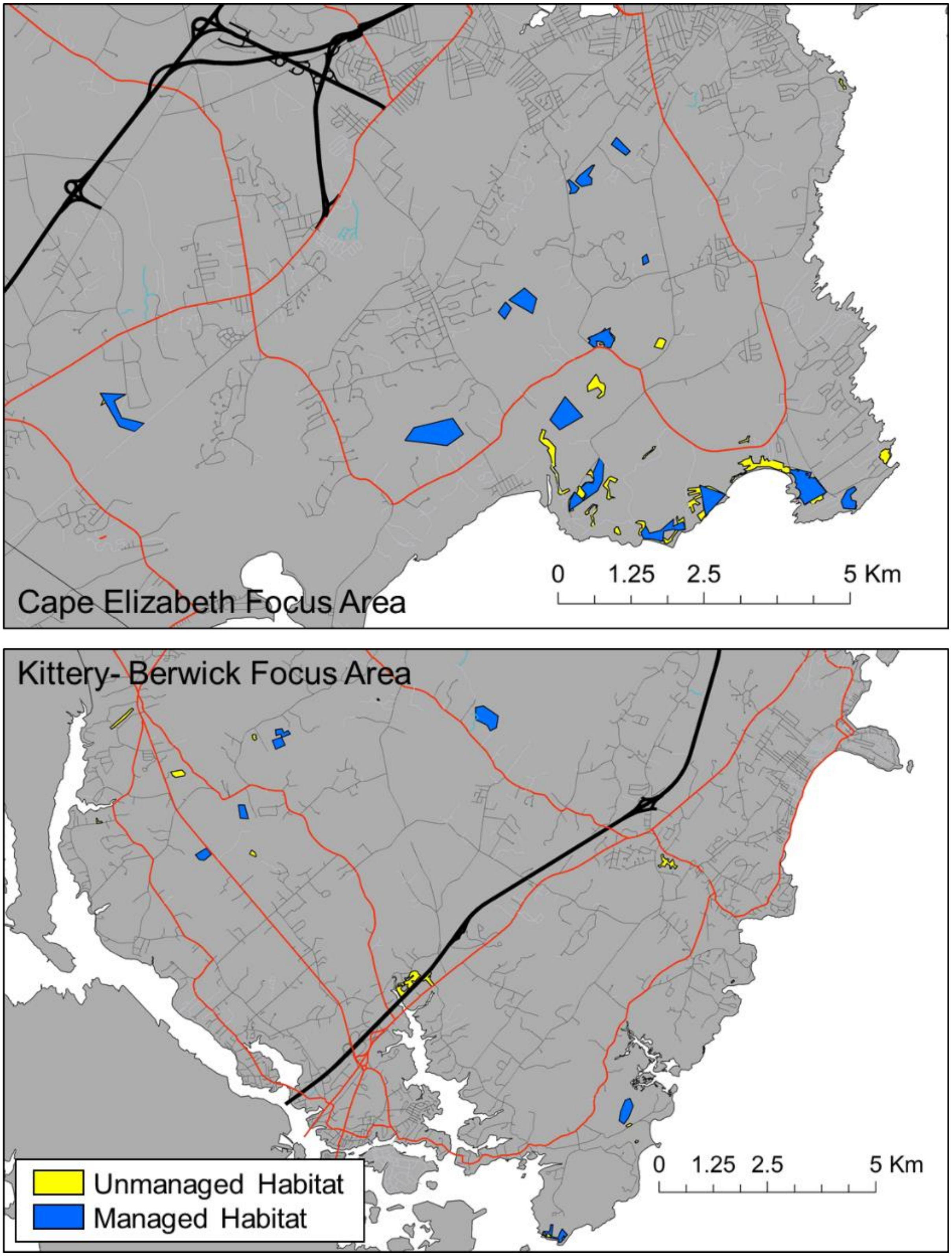

Figure 10: Habitat patches in the two focal areas, Cape Elizabeth and Kittery-Berwick. Managed habitat patches are shown in blue, and unmanaged patches in yellow.

Table 3. Managed and unmanaged habitats suitable for New England cottontails in two focal areas in southern Maine.

Focus Area	Managed/Unmanaged habitat patches Number	Mean size (ha)	Range (ha)	Mean distance between patches (km)
Cape Elizabeth	16/17	10.2/5.8	1.2-28.7/0.7-30.5	4.0
Kittery-Berwick	8/15	11.1/2.1	3.8-32.0/0.1-10.5	7.9

Model Vital Rates

To simulate metapopulation dynamics, vital rates including annual survival, dispersal distances, and recruitment were estimated using existing literature and unpublished research (Table 4). Information on juvenile survival rates of NEC is lacking. Therefore, I assumed juvenile rates to be equivalent to those of adults as reported in studies of other lagomorphs (e.g., Gillis 1998, Zeoli et al. 2008, Kielland et al. 2010). In the literature (summarized in Chapman and Litvaitis 2003), the number of young per year for various *Sylvilagus* species ranges from 14 to 39, with much variation in litter sizes and number of litters. Litter size and frequency can depend on the site suitability, age and size of the female, latitude (Chapman and Litvaitis 2003), and possibly a myriad of other factors. There are some NEC reproduction data from the captive breeding program at the Roger Williams Zoo (L. Perrotti, Roger Williams Zoo, Providence, RI; unpublished report), but it is unknown how captivity affects fecundity. Captive breeding programs are often hindered by lower survival and lower fertility than expected for the species (Snyder et. al, 1996). In the absence of real data on wild NEC reproduction, I have estimated recruitment to be 4.05 per individual, which is similar to other better studied *Sylvilagus* species (Chapman and Litvaitis 2003). Recruitment is calculated by multiplying the number of litters per year (3) × young per litter (9) × female proportion of the population (0.5) × annual survival rate (0.3).

Table 4. Estimated vital rates for New England cottontails used to parameterize the metapopulation model.

Vital rate	**Mean (SD)**	**Supporting literature**
Annual survival rate on patches ≥3 ha (source populations)	0.3 (0.15)	H. Kilpatrick (pers. comm.), Brown and Litvaitis (1995), Villafuerte and Litvaitis (1996)
Annual survival rate on patches <3 ha (sink populations)	0.15 (0.08)	H. Kilpatrick (pers. comm.), Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Carrying capacity	2 individuals per ha	Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Recruitment per capita on patches ≥3 ha (source populations)	4.05 (0.9)	Chapman and Litvaitis (2003), L. Perrotti (unpublished report)
Recruitment per capita on patches <3 ha (sink populations)	2.025 (0.45)	Chapman and Litvaitis (2003), L. Perrotti (unpublished report),Barbour and Litvaitis (1993)
Maximum dispersal distance	3 km	Litvaitis and Villafuerte (1996)
Maximum annual growth rate (λ)	2.0	Keith and Windberg (1978), Litvaitis and Villafuerte (1996)
Environmental Correlation	> 80%	Litvaitis and Villafuerte (1996)

Another model input is NEC abundance for each population or patch. There is some information on NEC density at occupied sites in Maine (e.g. Brubaker 2012). To be able to compare two focus areas, the NEC abundance data would need to be collected using the same methods and without bias for one area over another. There are ongoing efforts to standardize NEC monitoring protocols across the range (Fuller and Tur 2012), which would benefit modeling efforts that involve more than one focus area. I was not confident that I had current population data for all occupied patches in both focus areas. I chose to set all patches as occupied at the beginning of the simulations, to ensure that differences in predictions between focus areas and between management scenarios were not caused by differences in abundance data. While this may not be realistic, NEC abundance is highly dynamic, laborious to measure, and can be altered through translocations and reintroductions of rabbits, so I decided to maintain the focus of this analysis on habitat restoration by standardizing NEC abundance.

Model Structure

RAMAS GIS (Version 6, Akcakaya and Root 2013) provided the framework for developing a metapopulation model. Habitat availability, vital rates, demographic and environmental stochasticity, and environmental correlation were components of the model. Stochasticity included variation in annual survival, recruitment, and carrying capacity because these rates are affected by changes in weather, predation, and other factors. Based on the last 40 years of weather data from Portland, Maine, I found that snow persistence is highly variable (Fig. 11) and 1 in 10 winters had >100 days with snow on the ground (National Climatic Data Center 2015). NEC mortality is strongly influenced by long winters (Brown and Litvaitis 1995), and the depth and persistence of snow increase mortality in a similar species, eastern cottontail (*Sylvilagus floridanus*, Boland and Litvaitis 2008), so my model included a 10% annual probability of a catastrophe (severe winter) in which 75% of adults and juveniles die. In non-catastrophe years, the model adjusted vital rates based on a normal probability curve that is supported by snow-cover data that were normally distributed.

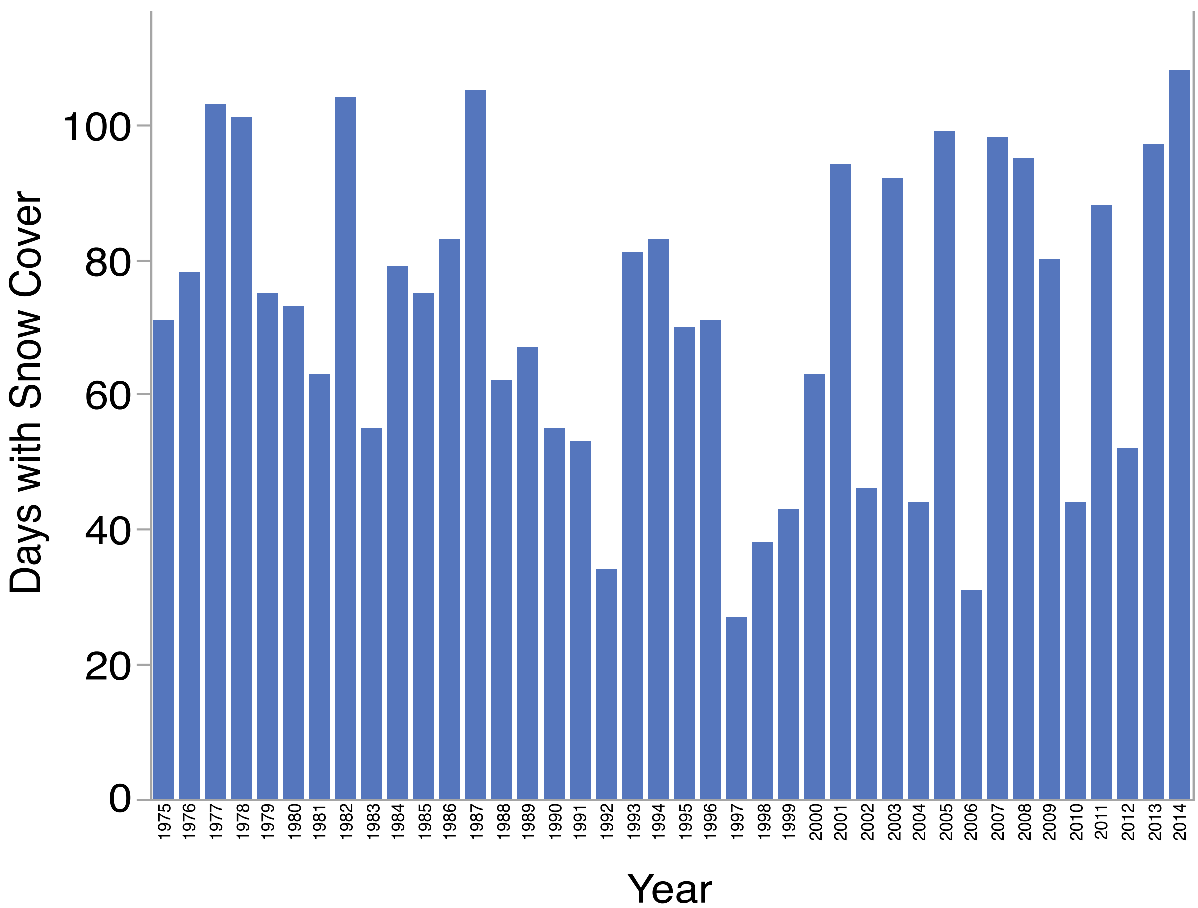

Figure 11: The number of days with snow cover each year from 1975 to 2014 in Portland, Maine, from the National Climatic Data Center (2015).

Environmental correlation is the effect of habitat patches close together responding similarly to events such as weather. NEC experience high environmental correlation (Litvaitis and Villafuerte 1996), as their vital rates are affected by weather and the metapopulations in northern New England are not large enough to experience significantly different weather events.

Inputs of habitat availability were modified to create five management alternatives (described below). For each scenario, I used a 15-year simulation that was replicated 10,000 times for both focus areas. Because variation is built into the model, each simulation is different, and a high number of simulations is needed to determine the average outcomes. Simulations more than 15 years may be unrealistic due to the ephemeral nature of the habitat and rapid life cycle of NEC. Metapopulation simulations generated two useful outputs: a population-growth trajectory and extinction risk. The trajectory showed an average abundance of NECs over time (increase or decline) whereas extinction risk was the proportion of the 10,000 simulations for a specific management plan that fell below a specified threshold of abundance.

Landscape suitability can be used to estimate the probability of dispersal between patches, e.g., NEC are more likely to reach a nearby patch if the intervening landscape is young forest rather than open fields or urban development. However, RAMAS GIS 6.0 cannot be used to calculate these probabilities due to GIS software changes since the inception of RAMAS GIS (N. Friedenberg, Applied Biomathematics, personal communication). Instead, I used geographic distances to estimate the probability of dispersal between patches. Dispersal is estimated using a probability curve, where individuals are more likely to disperse to patches that are closer, and do not disperse further than three kilometers (Litvaitis and Villafuerte 1996). A recent study (Cheeseman 2017) had an instance of a NEC traveling 3.8 km, but most dispersal distances recorded were under 2km and dispersal events were infrequent. It’s not certain how often NEC travel long distances, or how other factors affect the frequency and distance of dispersal, but as this is a growing area of research, I anticipate that more refined dispersal values will be available for use in future versions of this model.

Habitat Availability

Spatial information on unmanaged but suitable habitats was derived from a survey of known occupied habitat patches (Fenderson et al. 2014), completed in 2007-2009. Information on managed habitats was obtained in 2012 through 2014 from the Natural Resources Conservation Service, U.S. Fish and Wildlife Service, and Maine Department of Inland Fisheries and Wildlife. The amount and location of managed habitats was projected over the next 15 years based on the assumption that NEC habitats are ephemeral and require 7 years to become suitable after intensive management (e.g., clearcuts) and remain suitable for 10-12 years without further management (Aber 1979, Fig. 12). For each patch included in the models, I considered the initial condition, schedule of management actions, and the prescribed management activity, and then created maps of estimated suitable managed habitat for 4 time steps: the years 2015, 2020, 2025 and 2030. Based on field surveys (Fenderson et al. 2014), occupied patches did not need intensive management and were considered suitable at start of our simulations. Unmanaged and managed habitats were assumed to decline at a rate of 10% per year over the course of the simulation due to succession.

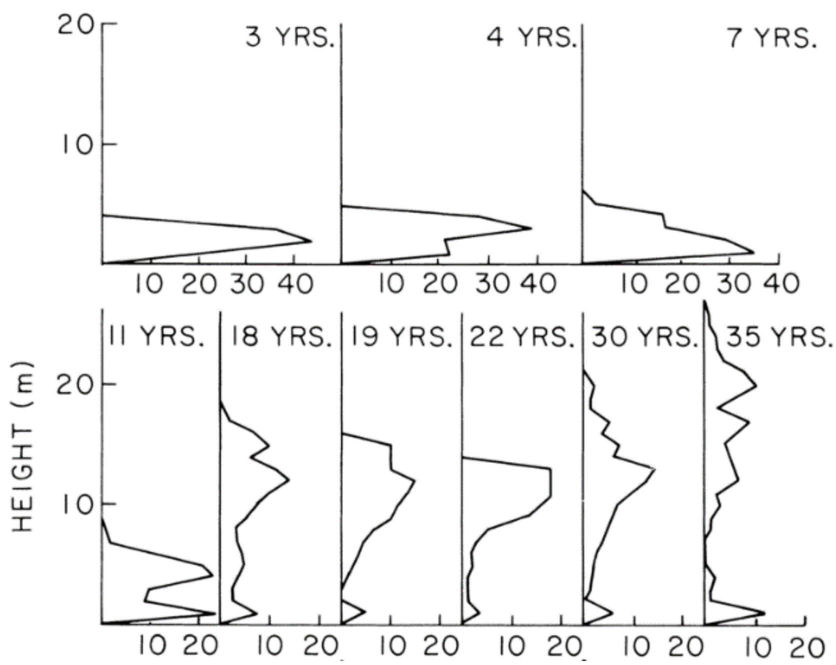

Figure 12. Vegetation regeneration in a hardwood forest after a clearcut (from Aber 1979). By 18 years after management, the bulk of the vegetation is no longer in the understory and the habitat is unsuitable for NEC.

<u>Management Alternatives</u>

I developed and compared the outcomes of five management scenarios in each focus area.

Scenario 1, no management: Only unmanaged habitat patches, based on known occupied sites, are considered suitable. This is representative of no action being taken to conserve NEC. Habitat availability declines due to succession over the course of the simulation.

Scenario 2, current management: Managed patches, based on current agency plans, are added to the unmanaged patches over time, but no further maintenance or management is invoked, so suitable habitat eventually declines with time. This scenario demonstrates the effects on NECs if the initiative to create and maintain habitat were to discontinue, causing a gradual decrease in available habitat.

Scenario 3, maintained management: All managed and unmanaged habitat patches are considered suitable for the duration of the simulation to represent continuous management of all patches. This represents the continued close monitoring and maintenance of all patches, if NEC habitat programs and funding continue and expand for the foreseeable future.

Scenario 4, maintained management with reintroductions: While all of these management scenarios include the assumption that NEC will be present on vacant, suitable patches either independently or through intervention at the beginning of the simulation, this scenario adds additional NEC re-introductions to patches throughout the simulation. Every 3 years, 5 adult NEC were added to all patches with less than 3 individuals.

Scenario 5, maintained management with additional large patch: Because larger habitat patches are associated with lower NEC mortality, land managers typically try to find and create larger management patches. This scenario examines the relative effect of adding a single, 50-ha patch to the center of each focus area.

<u>*Sensitivity Analysis*</u>

To examine the relative influence of specific model parameters on model output, values were modified by -50%, -25%, -10%, +10%, +25%, and +50% of the initial input value to measure the effects of these changes on the probability of falling below 50 individuals during the simulation (extinction risk). I chose to analyze five model parameters: the survival and recruitment rates, the standard deviations of the survival and recruitment rates, the probability that an individual disperses to another patch, the probability of environmental catastrophe (severe winters), and environmental correlation. Survival and recruitment were not analyzed separately because they are closely linked values: survival is a factor in determining recruitment, and both values make up the model's stage matrix. I chose not to analyze habitat availability, or the closely related carrying capacity, as that variable is the subject of manipulation under the management scenarios.

RESULTS

Focus Areas and Management Scenarios

Mean population trajectory, extinction risk, and the risk of falling below 50 individuals were calculated from the simulations for each focus area and each management scenario. Population trajectory is the abundance of NEC over time. Extinction risk is the probability of the metapopulation reaching zero individuals. Quasi-extinction is a threshold abundance below which the population is unlikely to recover, and the actual quasi-extinction abundance for these metapopulations of NEC are unknown. I chose to evaluate the likelihood of NEC abundance falling below 50 to represent quasi-extinction, because very small metapopulation sizes are a concern in addition to true extinction.

Simulations of the Cape Elizabeth metapopulation had higher abundances and lower extinction risks than those for the Kittery-Berwick metapopulation (Fig. 13, Table 5). However, the two metapopulations were affected similarly by each management scenario. The maintained habitat management scenario had a more stable trajectory, higher abundances, and lower extinction risks than the no management or current management scenarios. Adding in reintroductions of NEC, or an additional large source patch led to even better outcomes for both metapopulations.

All simulations have an initial drop in average abundance because the model calls for fully occupied patches at the beginning of the simulation, but the average abundance cannot be 100% of the carrying capacity once the populations are subjected to the varying survival rates, reproductive rates, and catastrophes. At times, many of the metapopulations may be approaching carrying capacity, which they cannot exceed, but the average abundance across the many simulations will always be less than the carrying capacity.

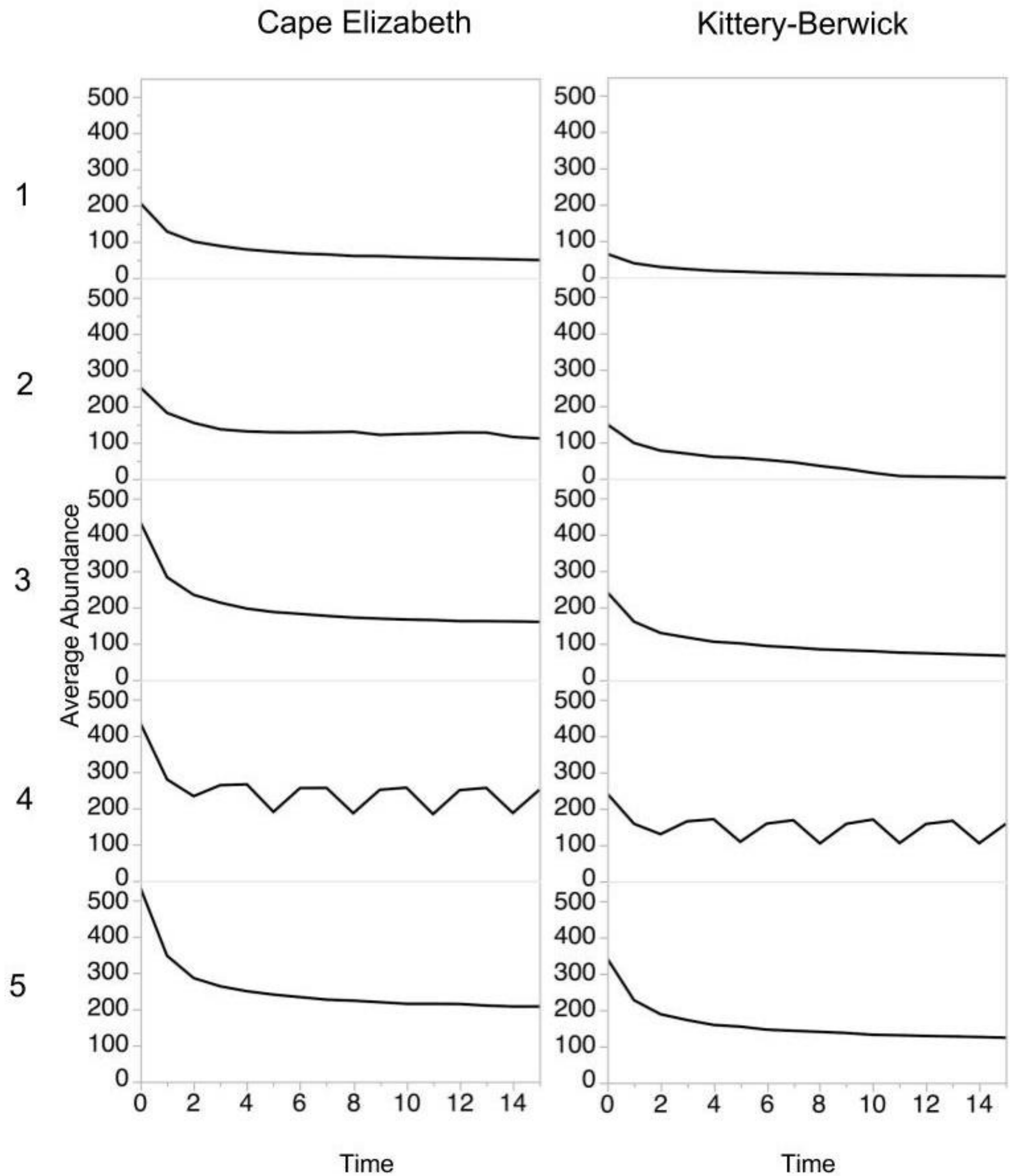

Figure 13: The population trajectory, or average abundance over time, of the model simulations for two focus areas, Cape Elizabeth and Kittery-Berwick, under five management scenarios, 1) no habitat management, 2) current habitat management, 3) maintained habitat management, 4) maintained habitat management with NEC reintroductions, 5) maintained management with additional source patch.

Table 5. Probability of falling below 50 or 0 individuals (extinction), and end mean abundance, after a 15-year simulation of five different management scenarios for Cape Elizabeth (CE) and Kittery-Berwick (KB) metapopulations.

Management Scenario	**Extinction CE/KB**	**< 50 individuals CE/KB**	**Mean abundance after 15 years CE/KB**
1: No Management	0.01 / 0.15	0.17 / 0.95	108.0 / 19.24
2: Current Management	0.0 / 0.14	0.04 / 0.95	181.1 / 20.04
3: Maintained Management	0.0 / 0.0	0.02 / 0.09	276.1 / 141.1
4: Maintained Management with Reintroductions	0.0 / 0.0	0.0 / 0.0	360.08 / 224.5
5: Maintained Management with Additional Source Patch	0.0 / 0.0	0.01 / 0.03	373.10 / 221.2

Sensitivity Analysis

Altering mean survival and recruitment rates, dispersal rates, or environmental correlation had little influence on the metapopulation extinction risks. However, increasing the variation (standard deviations) of survival and recruitment and the probability of catastrophe had a substantial influence (Fig. 14). These results suggest that the metapopulations are more responsive to demographic and environmental variation than to changes in mean vital rates and the proportion of dispersing individuals.

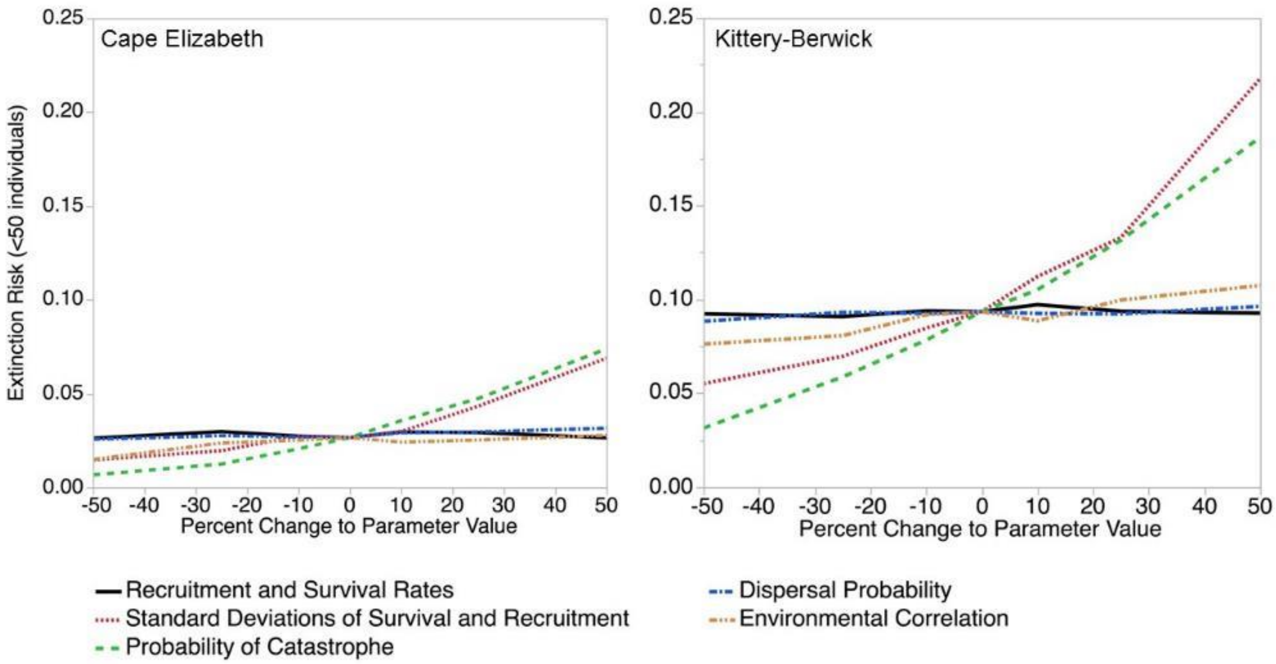

Figure 14. A sensitivity analysis of five parameters on both metapopulation models: recruitment and survival rates, standard deviations of recruitment and survival rates, probability of catastrophe (representing severe winters), dispersal rates (the proportion of the population that disperses to another patch), and environmental correlation.

DISCUSSION

Management Implications

Maintained management with reintroductions is the only management scenario that yielded zero extinction risk for both metapopulations. Generally, the two metapopulations benefitted from more intensive management scenarios, but there were differences in their responses. Notably, the Kittery-Berwick focus area had higher extinction risks and no improvement in outcomes between the no management and current management scenarios, whereas Cape Elizabeth had a very low extinction risk even with no management and had improved outcomes under current management. Both metapopulations had higher abundances and lower extinction risks under the hypothetical intensive management scenarios, maintained management with reintroductions and maintained management with additional source patch. Cape Elizabeth has more patches that are closer together, and had lower extinction risks and higher NEC abundances compared to Kittery-Berwick. This pattern supports the focus area strategy, which involves prioritizing habitat management near other patches. Both focus areas, but Kittery-Berwick in particular, will require hands-on management of habitat in order for NEC to persist in those areas.

The outcomes are similar to those of a metapopulation model for another early successional species, the ruffed grouse (*Bonasa umbellus*). The species is expected to continue to decline without habitat management intervention, and a model was used to compare management strategies at a landscape scale, in this case, creating few, large habitat blocks vs. several small blocks (Blomberg et. al 2012). Modeling of another species with which NEC has little in common, the Northern spotted owl (*Strix occidentalis caurina*), likewise found that large habitat patches that are close together could slow the decline of the metapopulation compared to other habitat configurations (Marcot et. al 2013), and it was determined that recolonization of vacant patches is important, much like NEC. Robinson (2013) modeled a metapopulation of swamp rabbits (*Sylvilagus aquaticus*), a species closely related to NEC but with a different habitat specialization, and found that small habitat patches act as population sinks, and catastrophic flooding was an important predictor of metapopulation decline. These results are similar to my findings that adding large habitat patches was beneficial to NEC persistence, and catastrophic mortality was an important model parameter.

Simulations with more habitat and greater initial NEC abundances have lower extinction risk and higher abundances throughout the simulation. It is logical that a higher carrying capacity, and thereby a higher potential abundance of NEC, would reduce the likelihood of metapopulation extinction. This underscores the importance of habitat management for NEC and other species that require early-successional habitat. The carrying capacity of the metapopulation can be increased by creating more habitat, or possibly by improving the suitability of existing habitat.

Habitat patch size is related to habitat quantity and quality, and carrying capacity. Benefits from adding a large patch to the focus areas support source-sink theory. Large habitat patches should be prioritized over more smaller ones. In my inventory of 196 reported NEC habitat management patches (Warren et al. 2016), 9 were stated as being below 3 hectares (considered a sink in this model), 104 were between 3 and 20 hectares, and 83 were larger than that. However, in conducting field work at 60 of these sites, I found that there was often a complex mosaic of varying suitability within these reported patches. Defining biologically relevant habitat patches is different from defining management parcels and would result in smaller patches in some cases. Managers should continue to prioritize the difficult task of not only securing large areas for NEC habitat management, but creating large, continuous patches of suitable habitat in these areas to increase carrying capacity and lower extinction risk for the metapopulation.

Variability and Climate Change

These models are stochastic, i.e., they incorporate environmental and demographic variability, causing each simulation to produce different results, in contrast to a deterministic model that only has one outcome. The sensitivity analysis showed that the model is influenced more by variation (in survival and recruitments, and catastrophes) than the other parameters. It was surprising that the model did not respond more to changes to the mean survival and recruitment rates; however, if these rates are decreased enough they eventually impact the outcome of the model, indicating that they are a limiting factor below a certain value and are therefore not completely inconsequential.

Increasing variation in the model increases extinction risk, which supports Boyce's (1977) findings that stochasticity negatively affects metapopulation persistence in models. This concept has implications for landscape scale conservation planning. Survival, dispersal, recruitment and other vital rates are affected by innumerable environmental and demographic factors. Our inability to predict the exact vital rates for a metapopulation into the future means that we should err on the side of caution when estimating the minimum habitat size, corridors, and population sizes needed for a metapopulation to persist. Real environmental and demographic variation, which could increase due to climate change and anthropogenic effects, are a detriment to metapopulation persistence (Pickett et al. 2015) and should not be underestimated in models.

Reviews of climate change studies state that weather will likely become increasingly variable, with more frequent, intense precipitation events, and in fact we are already seeing these effects today (e.g., American Association for the Advancement of Science 2014, Intergovernmental Panel on Climate Change 2014). This could have multiple impacts on NEC metapopulation growth and stability. If the range of vital rates increases in response to climate, and as catastrophic mortalities become more likely, the risk of metapopulation extinction is greater.

There may also be an increase in average winter temperatures that could reduce the average number of days per year with snow, benefitting NEC somewhat. However, I hypothesize based on my findings that NEC metapopulation extinction will be influenced more by environmental variability and the frequency of severe snowy winters than by small increases to annual survival rates. To mitigate this effect, populations of NEC and their habitat should be closely monitored so that managers can intervene when needed by introducing captive bred rabbits to vacant patches and maintaining and expanding suitable habitat.

Model Limitations and Research Needs

While these models are useful for comparing the relative effects of management scenarios, and for assessing the importance of different parameters on metapopulation persistence, there are several areas where more data would improve the predictions. In particular, the ability of these models to predict actual NEC abundance in the future is limited by a lack of actual NEC occupancy data, dispersal rates, and other vital rates. I have identified several areas for future research and model development to create more accurate predictions about NEC metapopulations.

RAMAS GIS version 6.0 calculates dispersal using geographic distances and does not incorporate landscape features that might facilitate or prevent dispersal. The body of literature on NEC dispersal is growing, and the models could be improved with dispersal probabilities based on real data, and even local, patch-specific data in some cases. For example, several barriers and facilitators of dispersal were identified using genetic methods (Amaral et. al 2016), and actual dispersal events have been recorded using telemetry (Cheeseman, 2017). The results of these studies are varied; for example, roads are known to be a barrier to NEC dispersal (Amaral et al. 2016, Cheeseman 2017), and NEC have been observed crossing roads, and are perhaps more likely to in certain landscape contexts (Cheeseman 2017), so the extent to which roads are a barrier and in what context requires more research to apply these findings to other landscapes. It is also important to acknowledge that some features that facilitate dispersal are as ephemeral as NEC habitat (e.g. abandoned fields and brushy road edges). Further studies of NEC dispersal over various landcover types, as well as how landcover types are changing, could help to build better spatial models of NEC metapopulations. In turn, these models could help land managers identify areas where the management of the landscape between patches would be needed to allow for successful dispersal.

The survival and recruitment values used in this model are the best current estimates. There are few studies on NEC survival rates and reproduction; NEC are difficult to track and observe in the wild. Variation in survival and recruitment rates is shown to be an important predictor of extinction risk in the sensitivity analysis, but without much larger sets of data, we cannot confirm that the amount of variation used in this model is accurate. A long-term study of NEC survival and recruitment at various sites would be needed to determine accurate mean survival and recruitment rates, standard deviations, and the probability of catastrophic mortalities. An additional factor that could affect these rates that is not represented in this model at all is the genetic isolation of each metapopulation.

Sensitivity analysis results can be used as a guide to focus research efforts on the most potentially influential model components. My sensitivity analysis suggests that variability and probability of catastrophe would be important parameters to research to improve the model. These values are difficult to measure, but the models can be useful despite our present uncertainty. When interpreting the results of the model, one must acknowledge that there is a wide range of possible trajectories NEC may follow and that extinction risk may be higher or lower than predicted, based partly on the accuracy of our estimates of variability and catastrophes, and other vital rates.

Although not included in the sensitivity analysis, habitat availability and suitability are important considerations for NEC persistence. When the suitability or quality of a habitat patch is known, the carrying capacity could be manually adjusted in the model, to reflect whether it could support a higher or lower density of NEC than the typical value of 2 per hectare. I focused my research on managed habitat patches, but surveys of the distribution and suitability of unmanaged habitat (occupied or not) across the range of NEC could be used in future models, and they could help to inform decisions about when and where to restore additional habitat.

Finally, these models could be verified by collecting data on NEC abundance in the same focus areas being modelled. Over time, the trend in actual abundance can be compared to the prediction. The model prediction is a summary of many possible futures, so it is not expected that the actual data will be an exact match; rather, data from many years in many locations can eventually reveal how accurate the model is.

Use of NEC Metapopulation Models as Decision-Making Tools

These models could be used to help make decisions about habitat restoration. They could be tailored to other focus areas, and location-specific information can be added, before comparing pertinent management scenarios. For example, a land manager might be interested to know where in their focus area adding a patch would be most valuable, or which patches would benefit most from reintroductions of captive bred rabbits. The following are several ways this model could be adapted and improved for use as a decision making tool for a specific area: Input dispersal probabilities based on firsthand knowledge of barriers, facilitators, and distance, or based on a GIS analysis of the area; adjust carrying capacities of the patches based on real NEC density data for those patches or based on knowledge of the patch's suitability; define the temporal changes in carrying capacity of the patches based on management plans (e.g. will all of the patches be maintained indefinitely? Or will some become unsuitable over time?). Spatial data of managed and unmanaged habitat within the focus area is also needed. Then, this model can be used to compare scenarios that the land manager is considering with more accuracy and locally relevant results.

Conclusions

In the metapopulation simulations, the Cape Elizabeth focus area had lower extinction risks and higher abundances of NEC than Kittery Berwick. More intensive management of habitat, and reintroductions of NEC, could improve metapopulation persistence. The focus area strategy, which involves prioritizing habitat restoration near other patches, is supported. The models I developed are sensitive to the variation in survival and recruitment (i.e., environmental variability), and the probability of catastrophe, suggesting that NEC metapopulations could be negatively impacted by variability and severe weather. Increasing frequency of severe winter storms with climate change could be a detriment to NEC survival, but this could be mitigated by monitoring and managing habitat, and reintroducing captive bred rabbits to vacant patches.

The models could be improved with more data and future research. Despite uncertainty about some of the model parameters, and, therefore, the accuracy of the predictions, these and other metapopulation models could be useful tools for land managers. Local data can be added (such as real data or estimates of dispersal between patches based on barriers and facilitators, carrying capacity of the patches, and the spatial distribution of managed and unmanaged habitat), for more locally relevant results. Then the model can be used to compare different management scenarios a land manager is considering.

REFERENCES

Aber, J. D. 1979. Foliage-height profiles and succession in Northern hardwood forests. Ecology 60:18–23. Ecological Society of America.

Akcakaya, H. R., M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjogren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. 2004. Species conservation and management: case studies. Oxford University Press, New York.

Akçakaya, H. R., J. Franklin, A. D. Syphard, and J. R. Stephenson. 2005. Viability of Bell's sage sparrow (*Amphispiza belli* ssp. Belli): altered fire regimes. Ecological Applications 15:521. Ecological Society of America.

Akcakaya, H. R., and W. T. Root. 2013. RAMAS GIS: Linking spatial data with population viability analysis (Version 6). Applied Biomathematics, Setauket, NY.

Amaral, K. E., M. Palace, K. O'Brien, L. E. Fenderson, A. I. Kovach. 2016. Anthropogenic habitats facilitate dispersal of an early-successional obligate: implications for restoration of an endangered ecosystem. PLoS ONE 11(3).

American Association for the Advancement of Science. 2014. What we know: the reality, risks, and response to climate change. Retrieved 23 September 2017 from http://whatweknow.aaas.org/wp-content/uploads/2014/07/whatweknow_website.pdf

Arbuthnot, M. 2008. A landowner's guide to New England cottontail habitat management. Environmental Defense Fund.

Barbour, M. S., and J. A. Litvaitis. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. Oecologia 95:321–327.

Blomberg, E. J., B. C. Tefft, J. M. Reed, and S. R. McWilliams. 2012. Evaluating spatially explicit viability of a declining ruffed grouse population. Journal of Wildlife Management 76:503–513.

Boland, Kelly M. and J. A. Litvaitis (2008). The role of predation and hunting on eastern cottontail mortality at Cape Cod National Seashore, Massachusetts. Canadian Journal of Zoology, 86:918-927.

Bowman, J., and J. F. Robitaille. 2005. An assessment of expert-based marten habitat models used for forest management in Ontario. Forestry Chronicle 81:801–807.

Brooks, R. P. 1997. Improving habitat suitability index models. Wildlife Society Bulletin 25:163–167.

Brown, A., and J. A. Litvaitis. 1995. Habitat features associated with predation of New England cottontails: what scale is appropriate? Canada Journal of Zoology 73:1005–1011.

Brubaker, D. R. 2012. Monitoring occupancy and abundance of New England cottontails using non-invasive genetic tools. Thesis. University of New Hampshire, Durham New Hampshire.

Burgman, M., D. Breininger, B. Duncan, and S. Ferson. 2001. Setting reliability bounds on habitat suitability indices. Ecological Applications 11:70–78.

Butler, B. J., and Z. Ma. 2011. Family forest owner trends in the northern United States. Northern Journal of Applied Forestry 28:13–18.

Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. Theoretical Population Biology 12:366-373.

Chapman, J. A. 1975. Sylvilagus transitionalis. Mammalian Species 55:1-4.

Chapman, J. A., and J. A. Litvaitis. 2003. Eastern cottontails and their allies. Pages 101–125 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America. Johns Hopkins University Press, Baltimore, MD, USA.

Chapman, J. A., K. L. Cramer, N. J. Dippenaar, and T. J. Robinson. 1992. Systematics and biogeography of the New England cottontail, Sylvilagus transitionalis (Bangs, 1895), with the description of a new species from the Appalachian Mountains. Proceedings of the Biological Society of Washington 105:841.

Cheeseman, A. 2017. Factors limiting recovery of New England cottontail in New York. Dissertation. State University of New York College of Environmental Science and Forestry, Syracuse New York.

Cook, J. G., and L. L. Irwin. 1985. Validation and modification of a habitat suitability model for pronghorns. Wildlife Society Bulletin 13:440–448.

Dalke, P. D., and P. R. Sime. 1941. Food habits of the eastern and New England cottontails. Journal of Wildlife Management 5:216–228.

Fenderson, L. E., A. I. Kovach, J. A. Litvaitis, and M. K. Litvaitis. 2011. Population genetic structure and history of fragmented remnant populations of the New England cottontail (Sylvilagus transitionalis). Conservation Genetics 12:943–958.

Fenderson, L. E., A. I. Kovach, J. A. Litvaitis, K. M. O'Brien, K. M. Boland, W. J. Jakubas. 2014. A multiscale analysis of gene flow for the New England cottontail, an imperiled habitat specialist in a fragmented landscape. Ecology and Evolution 4(10): 1853-1875.

Fickenscher, J. L., J. A. Litvaitis, T. D. Lee, and P. C. Johnson. 2014. Insect responses to invasive shrubs: Implications to managing thicket habitats in the northeastern United States. Forest Ecology and Management 322:127.

Fuller, S., and A. Tur. 2012. Conservation strategy for the New England Cottontail (Sylvilagus transitionalis). <http://www.newenglandcottontail.org/sites/default/files/research_documents/conservation_strategy_final_12-3-12.pdf>. Accessed 9 Jan 2013.

Germaine, S., D. Ignizio, D. Keinath, and H. Copeland. 2014. Predicting occupancy for pygmy rabbits in Wyoming: An independent evaluation of two species distribution models. Journal of Fish and Wildlife Management 5:298–314.

Gillis, E. 1998. Survival of juvenile hares during a cyclic population increase. Canadian Journal of Zoology 76 (10): 1949-1956.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Intergovernmental Panel on Climate Change. 2014. Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC.

Jackson, S. N. 1973. Distribution of cottontail rabbits (Sylvilagus spp.) in northern New England. M. S. Thesis, University of Connecticut, Storrs, USA.

Johnston, J. E. 1972. Identification and distribution of cottontail rabbits in southern New England. M. S. Thesis, University of Connecticut, Storrs, USA.

Keith, L. B., and L. A. Windberg. 1978. A Demographic analysis of the snowshoe hare cycle. Wildlife Monographs 58:1-70.

Kielland, K., K. Olson and E. Euskirchen 2010. Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. Canadian Journal of Forest Research 40: 1265-1272.

Levins, R.1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America, 15: 237-240.

Linkkila, T. E. 1971. Influence of habitat upon changes within the interspecific Connecticut cottontail population. M. S. Thesis, University of Connecticut, Storrs, USA.

Litvaitis, J. A. 1993. Response of early successional vertebrates to historic changes in land use. Conservation Biology 7:866–873.

Litvaitis, J. A. 2003. Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States? Forest Ecology and Management 185:113–126.

Litvaitis, J. A., M. S. Barbour, A. L. Brown, A. I. Kovach, J. D. Oehler, B. L. Probert, D. F. Smith, J. P. Tash, R.Villafuerte, and M. K. Litvaitis. 2007. Testing multiple hypotheses to identify the causes of the decline of a lagomorph species: the New England cottontail as a case study. Pages 167-185 in Biology of lagomorphs - evolution, ecology and conservation. P. C. Alves, N. Ferrand, and K. Hackländer, editors, Springer-Verlag, New York, USA.

Litvaitis, J. A., and W. Jakubas. 2004. New England cottontail (Sylvilagus transitionalis) assessment 2004. Maine Department of Inland Fisheries and Wildlife, Bangor, USA.

Litvaitis, J. A., B. Johnson, W. Jakubas, and K. Morris. 2003. Distribution and habitat features associated with remnant populations of New England cottontails in Maine. Canadian Journal of Zoology 81:877–887.

Litvaitis, J. A., J. L. Norment, K. Boland, K. O'Brien, R. Stevens, D. Keirstead, T. Lee, J. D. Oehler, J. M. Taylor, S. Bickford, and M. D. Tarr. 2013. Toward consensus-based actions that balance invasive plant management and conservation of at-risk fauna. Environmental Management 52:1313–1319.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1985. A comparison of methods used to examine snowshoe hare habitat use. Journal of Wildlife Management 49:693–695.

Litvaitis, J. A., J. P. Tash, M. K. Litvaitis, M. N. Marchand, A. I. Kovach, and R. Innes. 2006. A range-wide survey to determine the current distribution of New England cottontails. Wildlife Society Bulletin 34:1190–1197.

Litvaitis, J. A., and R. Villafuerte. 1996. Factors affecting the persistence of New England cottontail metapopulations: the role of habitat management. Wildlife Society Bulletin 24:686–693.

Litvaitis, J . A., D. L. Wagner, J. L. Confer, M. D. Tarr, and E. J. Snyder. 1999. Early successional forests and shrub-dominated habitats: land-use artifact or critical community in the northeastern United States? Northeast Wildlife 54:101-118.

Marcot, Bruce G, M.G. Raphael, N.H. Schumaker, B. Galleher. 2013. How big and how close? Habitat patch size and spacing to conserve a threatened species. Natural Resource Modeling 26: 194-214.

McComb, W. C., J. R. Sedell, and T. D. Buchholz. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273–281.

National Climatic Data Center. 2015. Snow Depth, Portland International Jetport, ME, US.

Nudds, T. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

Pickett, E. J., D. L. Thomson, T. A. Li, and S. Xing. 2015. Jensen's inequality and the impact of short-term environmental variability on long-term population growth rates. PLoS ONE 10(9): e0136072.

Probert, B. L., and J. A. Litvaitis. 1996. Behavioral interactions between invading and endemic lagomorphs: Implications for conserving a declining species. Biological Conservation 76:289–295.

Robel, R. J., L. B. Fox, and K. E. Kemp. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. Wildlife Society Bulletin 21:415–421.

Robinson, Christopher. 2013. Metapopulation viability of swamp rabbits (Sylvilagus aquaticus) in southern Illinois. Thesis. University of Southern Illinois, Carbondale.

Roloff, G. J., and B. J. Kernohan. 1999. Evaluating suitability reliability index of models. Wildlife Society Bulletin 27:973–985.

Schamberger, M., and W. B. Krohn. 1982. Status of the habitat evaluation procedures. Transactions of the North American Wildlife and Natural Resources Conference 47:154–164.

Smith, D. F., and J. A. Litvaitis. 2000. Foraging strategies of sympatric lagomorphs: implications for differential success in fragmented landscapes. Canadian Journal of Zoology 78:2134–2141.

Snyder, N., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10: 338-348.

Tash, J., and J. A. Litvaitis. 2007. Characteristics of occupied habitats and identification of sites for restoration and translocation of New England cottontail populations. Biological Conservation 137:584–598.

Terrell, J., and J. Carpenter. 1997. Selected habitat suitability-index model evaluations. US Geological Survey Biological Resources Division Technical Reports Series, Information and Technology Report 1997-0005, Washington D.C., USA.

USFWS (United States Fish and Wildlife Service). 1981. Ecological Services Manual. U.S. Government Printing Office, Washington DC.

USFWS (United States Fish and Wildlife Service). 1989. Animal Notice of Review. Federal Register 54:554-579.

USFWS (United States Fish and Wildlife Service). 2015. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List the New England Cottontail as an Endangered or Threatened Species. Federal Register 80:55286-55304.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901

Villafuerte, R., J. A. Litvaitis, and D. F. Smith. 1997. Physiological responses by lagomorphs to resource limitations imposed by habitat fragmentation: implications for condition-sensitive predation. Canadian Journal of Zoology.

Warren, A. , J. A. Litvaitis, D. Keirstead. 2016 Developing a habitat suitability index to guide restoration of New England cottontail habitats. Wildlife Society Bulletin 40: 69-77.

Zeoli, L. F., R. Saylor, and R Wielgus 2008. Population viability analysis for captive breeding and reintroduction of the endangered Columbia basin pygmy rabbit. Animal Conservation 11: 504-512.

APPENDICES

APPENDIX A: HSI User Guide

Habitat Suitability Index

For

Managed New England Cottontail Habitat

User's Guide

Alena Warren

Introduction

As part of an effort to conserve the species, habitat is being created, restored or maintained for New England cottontails (NEC) across New England and New York. Management practices include clearcutting, selective cutting, burning, removing invasives, and planting shrubs and trees. Management occurs on a variety of types of sites (e.g. old fields, forests, and coastal shrublands). Despite the diversity among managed habitat patches, the common goal is to create large patches of suitable NEC habitat, that consist of dense woody understory vegetation, presence of refuges, and access to herbaceous forage.

To evaluate the suitability of managed sites, a Habitat Suitability Index (HSI) was developed. An HSI is a model that incorporates all of the important habitat components (food, water, nesting areas, etc) for a species, and combines them to generate a suitability score for the site from 0 to 1. An HSI for NEC has been created to help guide the management of NEC habitat sites. Evaluating a site using this method can aid land managers in deciding how and when to manage a site and determine whether it is suitable for NEC.

When to use this model

This model is intended to be used on sites that have been selected for NEC habitat management. It is not intended to be used at a landscape scale or to identify potential NEC habitat management sites. It is assumed that before applying the HSI, the land manager has already determined that the site is large enough to accommodate NECs, and is in a suitable location on the landscape (e.g., is near other NEC habitat patches, the surrounding area is not overly hostile to NEC, etc.).

This model can be used as a baseline before management in some cases, and may be useful for planning purposes. Due to the successional nature of NEC habitat, a site should be monitored using this method every 2-3 years or as the manager sees fit to determine whether a site is becoming more suitable or less suitable over time. The suitability score generated by the HSI can help a land manager decide when it is time to intervene and manipulate a site again.

This method provides a standardized measure of site suitability so that sites can be compared to one another. This is particularly useful in areas where an agency may be selecting sites to release captive bred NEC onto. The agency can assess the potential sites using the HSI and easily compare the suitability scores to one another in order to select the best site available for release.

HSI Overview

The HSI for managed NEC habitat was developed based on previous NEC studies, expert opinion, and field data collected from NEC management sites. There are five habitat variables that are assessed (Table A1). Each variable is converted into a score from 0-1, and then the five scores are combined in the HSI model to generate a 0-1 score for the site.

Table A1: Habitat variables used in the New England cottontail Habitat Suitability Index

Variable	**Definition**
V_1: Security cover	Percentage of the woody vegetation that has a cover density of >300,000 stem- cover units/ha
V_2: Other cover	Percentage of the woody vegetation that has a cover density of 100,000-300,000 stem-cover units/ha
V_3: Height of woody cover	Average height of the woody understory vegetation in the patch (meters)
V_4: Summer forage	Edge-to-area ratio of grassy openings to woody cover (meters/ha)
V_5: Additional refuges	Presence/absence of constructed brush piles, artificial burrows, rock walls, and stone foundations

The HSI model is as follows, where the 0-1 score for each variable is used, except for V5 (refuges), which can only be 0 or 0.1:

$$HSI = \frac{3^* V1 + 2^* V2 + V3 + V4}{7} + V5$$

Where:
V1 = Security cover
V2 = Other cover
V3 = Vegetation height
V4 = Summer forage
V5= Refuges

<u>Data Collection</u>

Variables 1, 2, and 3

Variable 1: Security Cover, is the coverage of the woody vegetation on the site that is very dense. Very dense is defined as over 300,000 stem-cover units /ha. Variable 2, other cover, is the percentage of the woody vegetation that is moderately dense, or between 100,000 and 300,00 stem-cover units/ha. A stem-cover unit is the relative amount of cover provided by a type of plant (Table A2), for example, honeysuckle species tend to provide more cover per stem than a raspberry. This variable is measured by counting and identifying stems in sample plots. Variable 3 is the height of the woody understory vegetation, measured in meters. At each sample plot used to quantify cover density, the dominant height is also measured and then averaged for the site.

Table A2: The plant groups for which cover-units have been developed.

Plant Group	Cover-Units per Stem
Eleagnus	13.16
Berberis	8.72
Cornus	4.28
Evergreen trees	65.88
Lonicera	31.09
Juniperus	14.07
Low-growing shrubs	2.63
Rubus	1.00
Rosa	5.81
Spirea	1.88
Deciduous trees	2.65
Upright shrubs	6.56

First, delineate the patch's boundary using spatial software such as Google Earth or ArcMap. Plots will be 10x1 m, laid out perpendicular to and centered on transects. The transects and sample plots can be located in the field using a meter tape and compass (Method 1) or ahead of time using aerial photography and a GPS (Method 2), details on each approach are below and illustrated in Fig. A1.

Method 1: Transects are laid out North to south, unless the shape of the site is better suited to another orientation. Starting in the southwest corner, 10 m away from any edge of the patch, begin a transect heading North. Measure 30 m using a meter tape. At the 30 m mark, lay out a 10x1 msample plot centered on the transect and perpendicular. This can be achieved using a 5 m rope and 1m fiberglass rod or pvc pipe, or a measuring tape and flags. Repeat this process every 30m along the transect, remaining >10m from all edges. Begin the next transect 100m away and parallel to the first, and repeat until the entire site has been covered. If the site is a very irregular shape or very small, the transects may need to be 50 m apart instead of 100 in order to locate several usable plots.

Method 2: Using Google Earth, ArcMap, or a similar program, make a set of points that will be the sample plot locations. Using the guidelines from method 1 (transects 100 m apart and plots every 30 m) can help to streamline data collection if the site is difficult to traverse, compared to placing the plots along a square grid. The sample plots should all be at least 10 m from any edge, and there should be a sufficient number of plots based on the size of the site. Load the points onto a GPS to locate the sample plots in the field. At each point, lay out the 10x1 m sample plot area in a west to east orientation. This can be achieved using a 5m rope and 1 m fiberglass rod or pvc pipe, or a measuring tape and flags.

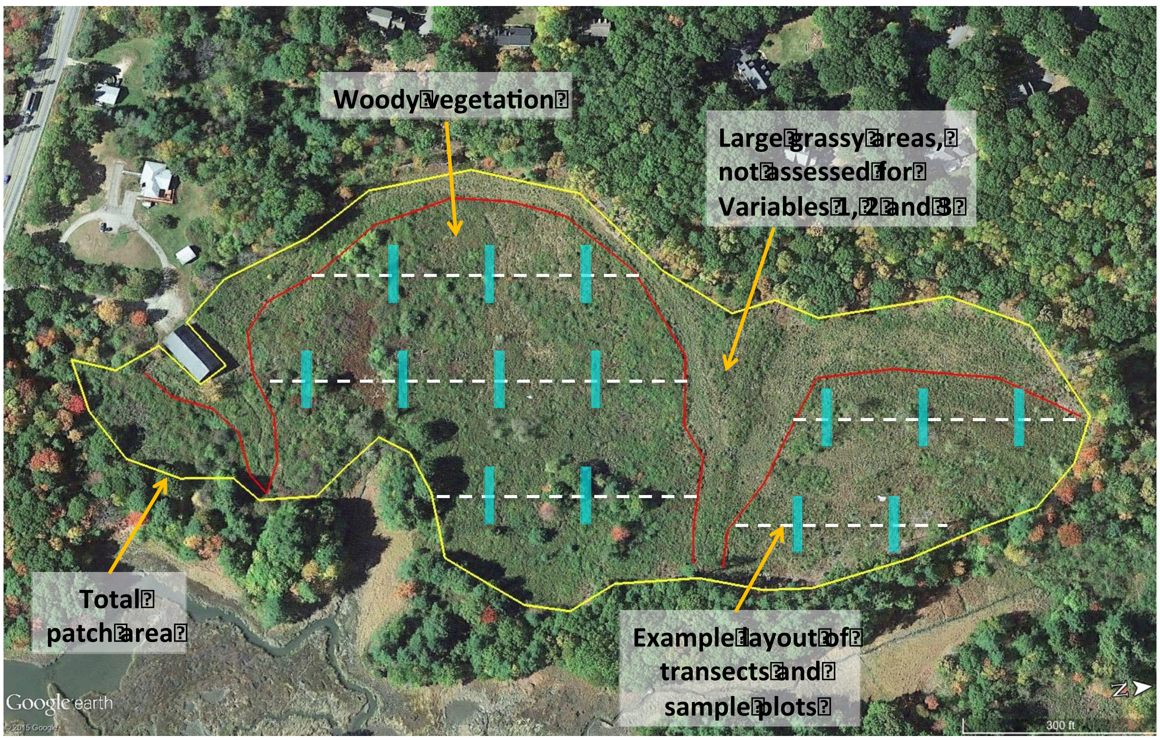

Figure A1: Example of transect and sample plot layout at a site. Large areas with no woody vegetation, or with closed-canopy forest, are not included.

At each sample plot, the woody plant stems are inventoried. Woody stems should be counted if they are at least 0.5 m tall, and less than 7.5 cm DBH. Stems should be counted at ground-level, that is, if a stem splits into multiple stems above the ground, it should be counted as one (or however many stems are emerging from the soil). If some stems fall directly on the boundary of the plot, count every other one.

Identify the plant group (Table A2) that the stem belongs to, in order to convert the stem count to a stem-cover unit density later on. Use the data sheet provided (Appendix C) or similar. Visually assess the height of the vegetation in the plot area and measure the dominant height (representing the height of most of the vegetation, not necessarily the height of the tallest vegetation). Document the height in meters for each plot.

For each sample plot, find the stem-cover unit density using either a spreadsheet with embedded formulas, or manually by multiplying the stem count of each plant group by its cover-unit multiplier (Table A2). Then, find the percentage of plots with a density of >300,000 (Variable 1, security cover), and the percentage of plots with a density of 100,000 to 300,000 (Variable 2, other cover). Average all of the sample plot heights for Variable 3, Height.

Variable 4: Summer Forage

NEC utilize grass, legumes and other herbaceous growth for food during the growing season if it is near protective cover. Access to herbaceous forage on a site is measured as the edge to area ratio of grassy openings to protective cover. This is calculated using high resolution current aerial imagery, and a software program such as Google Earth or ArcMap. Usually the imagery available on Google Earth or Bing is sufficient, if other photography sets are not available. As NEC habitat sites are successional, and the site being evaluated may have been managed recently, it is important to verify the accuracy of the imagery in the field.

To calculate edge, delineate the edges between woody vegetation that serves as cover (shrubs, young trees and vines) and grassy openings that lack woody vegetation. Measure the edge in meters. Ignore grassy openings that are less than 3 m across in any direction, as these will likely soon be overtaken by woody vegetation and likely don't provide significant foraging opportunities due to being shaded and small in size.

The area of the patch (in hectares) can also be calculated using aerial photography. Exclude areas obviously not used by NEC such as mature forest, large fields, etc. Sometimes the edge between cover and forage can also be the boundary of the patch, for example, if a shrub-dominated area borders a large grassy meadow. NEC likely only use the edge of the meadow, so it's not appropriate to include the entire meadow in the patch area.

To calculate the edge to area ratio of grassy openings to cover, divide the length of edge (meters) by the patch area (hectares).

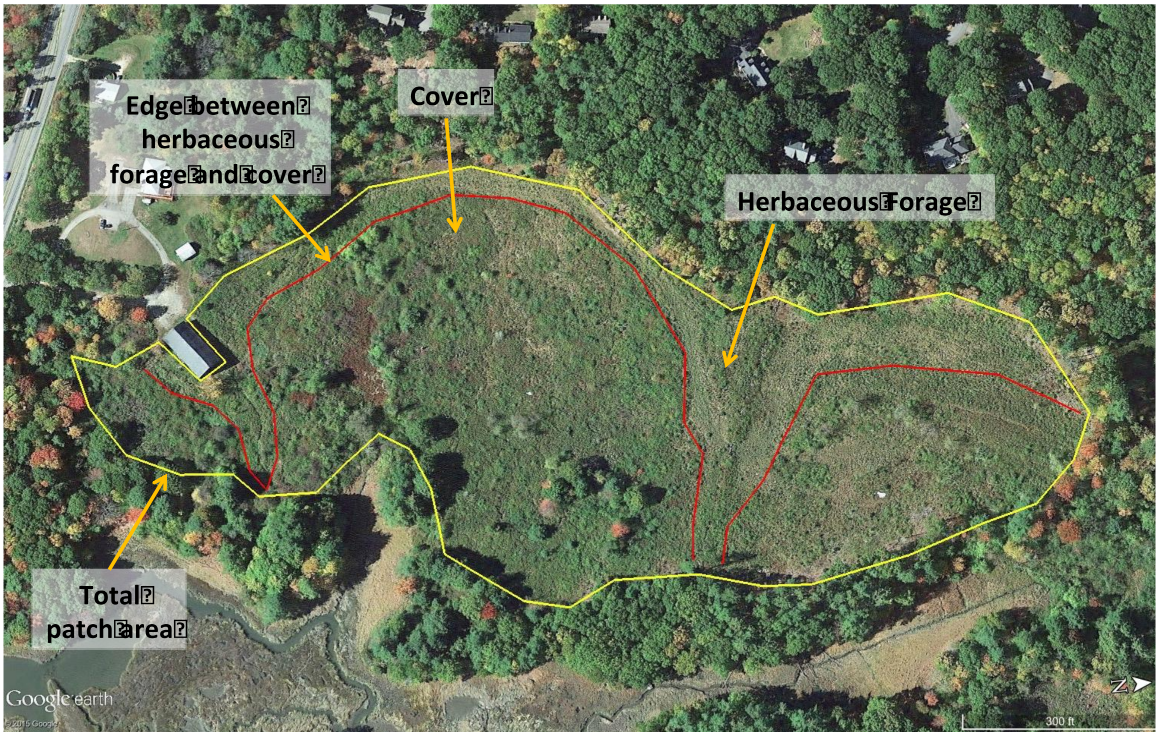

Figure A2: An example of using Google Earth to delineate the edge between herbaceous forage and protective cover, and the total patch area. The edge is shown in red, and the patch boundary in yellow.

Variable 5: Refuges

Variable 5 is the presence of refuges that NEC might use for additional protection. These include stone foundations and walls, brush piles (Fig. A3), burrows left by other animals, and artificial burrows. While sampling for variables 1-3, make note of any refuges seen. On sites where there is abundant dense woody vegetation, it is much more difficult to detect refuges, so this variable is measured as the presence or absence of refuges rather than a density of refuges.

Figure A3: A brush pile created to provide refuge for NEC.

Entering data into the model

The measurements found for variables 1-5 are converted into 0-1 scores. For Variables 1-4, suitability curves have been developed for this purpose (Fig. A4). Simply identify the measurement found for the site on the x-axis and find the corresponding 0-1 value, or use a spreadsheet with these functions embedded to automatically calculate the scores. Variable 5 does not have a suitability score, instead, this variable equals 0.1 if refuges were found on the site, and 0 if not.

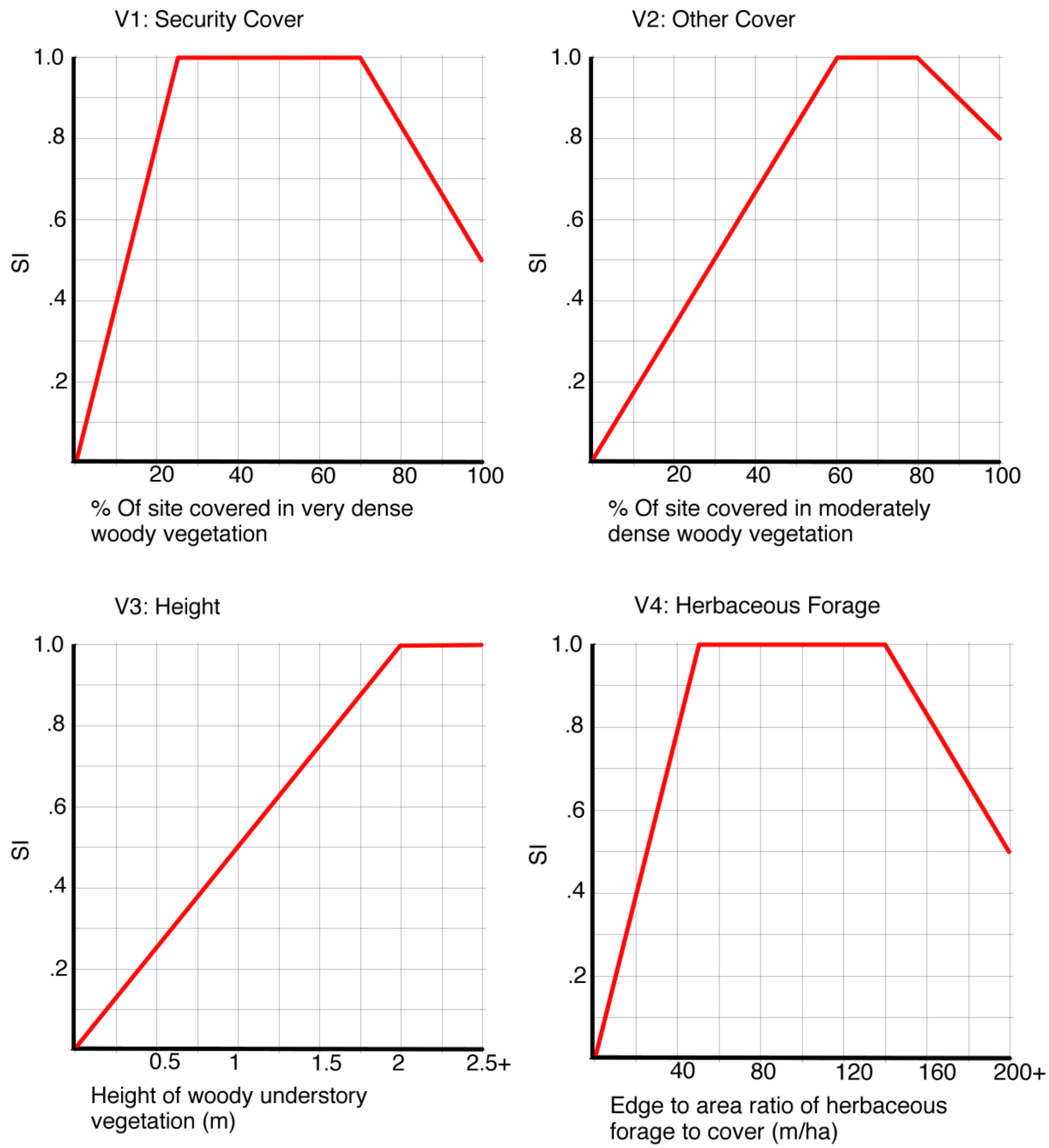

Figure A4: Suitability index curves, used to convert the measurements of variables 1-4 into suitability scores from 0 to 1.

Then, the scores for the 5 variables are combined in a weighted average to generate a 0-1 score for the site:

$$HSI = \frac{3 * V1 + 2 * V2 + V3 + V4}{7} + V5$$

Where:
V1 = Security cover
V2 = Other cover
V3 = Vegetation height
V4 = Summer forage
V5= Refuges

Interpreting HSI Scores

The HSI score provides a quantitative measurement for comparing sites to one another, and to monitor a site over time. If a site's score begins to drop, it may be time to implement management practices. Recalculating the score every 2-3 years will help managers identify the point in time when a site becomes too overgrown for NEC. The individual variable scores provide insight into which habitat component requires improvement. When considering where to release captive bred NEC, managers could compare the HSI scores of all of the potential habitat patches in the area of interest.

APPENDIX B: Developing Cover Values for Plant Groups

New England cottontails require dense woody cover. This habitat feature is often measured by counting woody stems (e.g., Litvaitis, Sherburne, & Bissonette, 1985). However, the amount of cover provided by a single woody stem varies, depending partly on the species and height of the plant. Barbour and Litvaitis acknowledged this by assigning “stem cover units” which weighted coniferous stems more heavily than deciduous stems in their stem counts (Barbour and Litvaitis 1993). To further refine the estimated cover provided by different species, species commonly found in NEC habitat were divided into groups by structural similarities as illustrated in Figure B1, and analyzed with a profile density board (Nudds 1977).

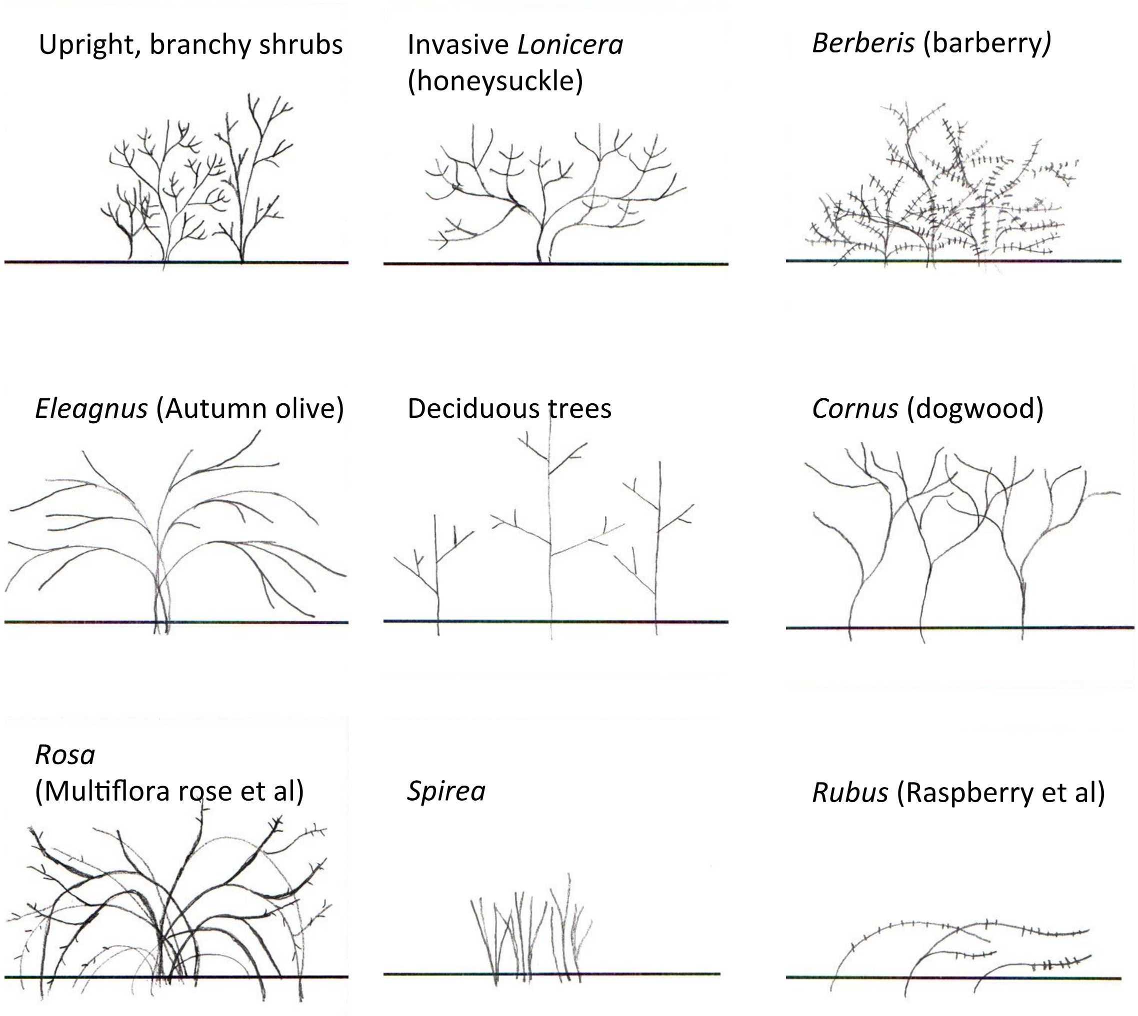

Figure B1: Several of the plant groupings used to evaluate cover per stem.

Ten sites known to have diverse vegetation suitable for NEC in Strafford county NH, Rockingham county NH, and York county ME were used as the study sites. At each site, samples from each of the plant groups were identified and measured. A sample is defined as a homogenous shrub, clump, or stand of woody vegetation that meets size criteria: height between 1m and 4m, and DBH under 7cm. For each sample, visual obstruction was estimated with a profile board (0.33 x 2 m) in 0.5 meter vertical quadrants from a distance of 5 meters, adapted from Nudds (1977). Species, number of stems, and height were also recorded. 478 total samples were collected.

To determine the relative amount of cover provided by each group of plants, the % of the board obstructed was plotted against the number of stems for each sample. Then, a line was fitted to the points that was constrained to a y-intercept of 0 (because 0 stems should yield 0% of the board obstructed). The slope of this line represents the obstruction, or cover, that each additional stem in the sample provides. These slopes were used to derive a cover coefficient (Table B1) that can be used to weight stem counts, much like Barbour and Litvaitis did with stem cover units (Barbour and Litvaitis 1993). All slopes were divided by the value of the least slope, so that the group providing the least amount of cover by stem has a weight of 1 and all other groups are greater than 1.

This data is being used to more accurately estimate the cover at a NEC habitat patch. The coefficients are applied to the stem counts collected, generating a “weighted” stem count for the site. Because a coefficient of 1 is assigned to the group providing the least cover, *Rubus*, it is difficult to compare the weighted stem count to a traditional stem count, and the traditional stem density thresholds (e.g., over 40,000 stems per ha provides sufficient cover for NEC) should not be applied. To avoid confusion, the weighted stem count for a plot or a site is referred to as the cover value.

Table B1: The slopes and cover values of the plant groups analyzed.

Group	Slope of Line	Cover Value
Eleagnus	5.66	13.16
Berberis	3.75	8.72
Cornus	1.84	4.28
Evergreen trees	28.33	65.88
Lonicera	13.37	31.09
Juniperus	6.05	14.07
Low-growing shrubs	1.13	2.63
Rubus	0.43	1.00
Rosa	2.50	5.81
Spirea	0.81	1.88
Deciduous trees	1.14	2.65
Upright shrubs	2.82	6.56

Appendix C: Example field data collection sheet

Site	Plot ID	Height	Refuges	Trees	Misc Nat. shrubs	Rose	Honey-suckle	A. Olive	Juniper	Rubus	Laurel/ Rhod	Bar-berry	Spirea	Ever-green Trees	Low Shrubs	Misc Inv. Shrubs	Native Vines	Inv. Vines	Dogwood	Inv. Trees	Notes
	4																				
	5																				
	6																				
	7																				
	8																				
	9																				
	10																				
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