

FINAL REPORT
for
Habitat Monitoring and Evaluation of Working Lands for Wildlife:
New England Cottontails

Prepared by

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SUMMARY BY STUDY OBJECTIVES

OBJECTIVE I -- DEVELOP A HABITAT MONITORING PROTOCOL FOR NEW ENGLAND COTTONTAILS THAT EVALUATES MANAGEMENT ACTIVITIES RELATIVE TO SUITABILITY AT THE SITE-SPECIFIC SCALE.

Approach: Generate habitat suitability index (HSI) equation using field data and expert opinion.

A manuscript on this approach has been accepted for publication by the Wildlife Society Bulletin (Appendix A).

OBJECTIVE II -- EVALUATE THE EFFECTS OF HABITAT MANAGEMENT AT THE LANDSCAPE SCALE USING POPULATION VIABILITY ANALYSES.

Approach: Use demographic information on New England cottontails and several scenarios on habitat management to explore the role of vital rates and habitat management in maintaining cottontail metapopulations.

INTRODUCTION

In response to the range-wide 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. 1). This strategy, although intuitive, is untested. Metapopulation modeling offers an approach to evaluating its potential success. A metapopulation is a set of local populations that interact with one another via dispersal. Management focus areas will likely function as metapopulations where *source* and *sink* populations determine its viability (Fig. 2). A source population has high survival rates from which individuals frequently disperse to other populations. Sink populations, on the other

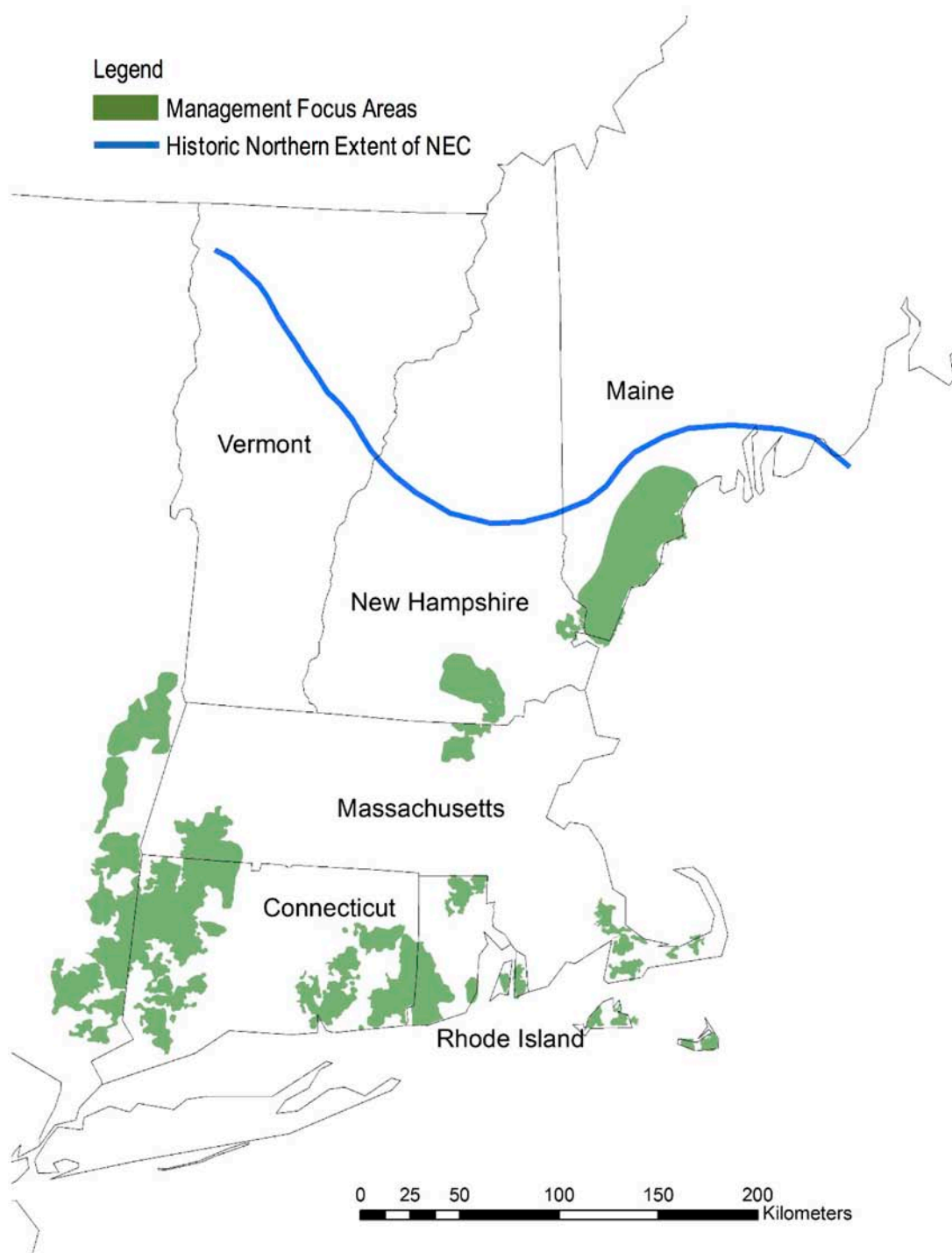


Figure 1. The approximate historic northern extent of New England cottontails in northern New England, and the current management focus areas (Fuller and Tur 2012).

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 (Akçakaya et al. 2004). Modeling is commonly used in such efforts because it provides an opportunity to conduct simulations that would not be feasible otherwise. It would require immense resources and time to conduct a real experiment in which habitat availability was manipulated to determine the effects on population growth of NEC.

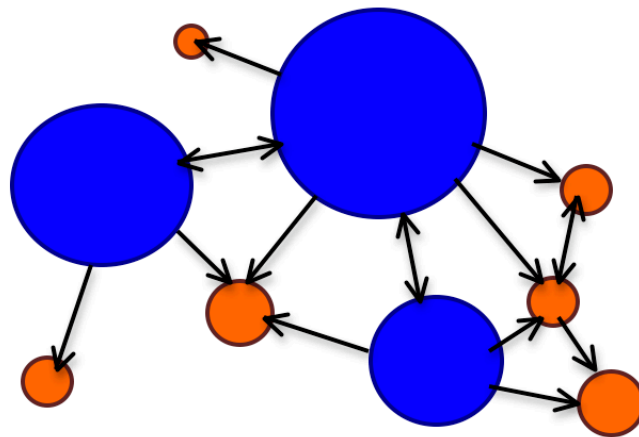


Figure 2. Illustrated metapopulation composed of source patches (blue) and sink patches (orange), where the size of the circle represents carrying capacity. Source patches supply dispersing individuals that colonize sink patches, which are vulnerable to population decline and extinction.

Further, a metapopulation model can be used for population viability analyses (PVA) to examine population growth and extinction probabilities in response to various management alternatives (Akçakaya et al. 2004, Blomberg et al. 2012). A PVA often includes population-specific vital rates and demographic/environmental stochasticity making it more realistic than population estimates based simply on habitat availability (Akçakaya et al. 2005). 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. These investigators found that fewer large patches resulted in a slower population decline (Blomberg et al.

2012). Modelling a hypothetical 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).

To understand how restoration activities at the landscape scale will affect population growth and stability of NEC, we examined the effects of habitat management and environmental variation on two existing NEC metapopulations. Specifically, we examined the influence of three management scenarios (no management, creation of suitable habitat but no maintenance of habitats, and creation and maintenance of suitable habitats) on viability of two NEC metapopulations in established focus areas. We also evaluated the relative influence of demographic and environmental parameters on model output using sensitivity analyses. Combined, these results enabled us to critique current activities to restore existing NEC metapopulations.

METHODS

Study Areas

We modeled the Cape Elizabeth, Maine and Kittery-Berwick, Maine (Fig. 3) focus areas because there has been considerable information on NEC populations in those landscapes (Litvaitis et al. 2003, Fenderson et al. 2014).

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 1). 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 1).

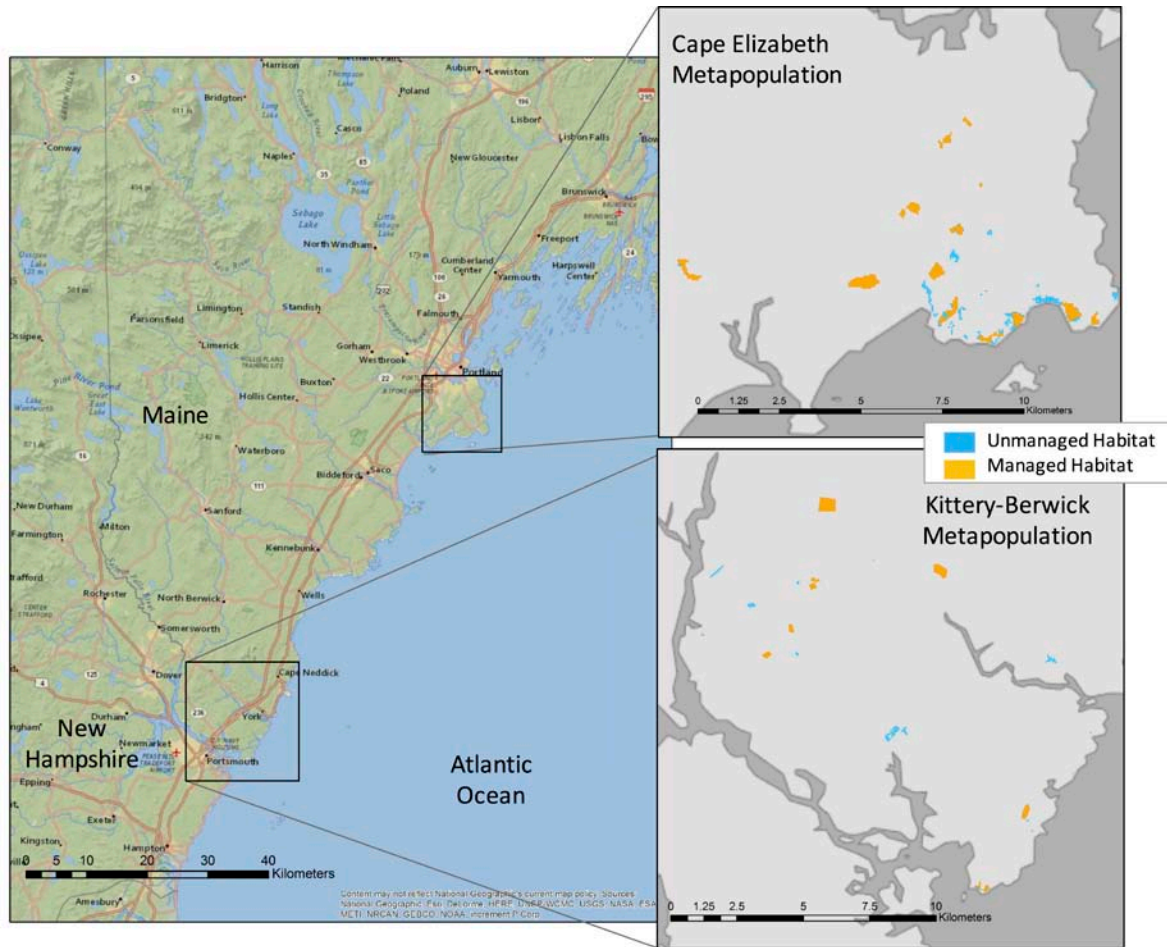


Figure 3: Habitat patches in the two focal areas, Cape Elizabeth and Kittery-Berwick, and the locations of the focal areas in Southern Maine. Managed habitat patches are shown in orange, and unmanaged patches in blue.

Table 1. Managed and unmanaged habitats suitable for New England cottontails in two focal areas in southern Maine.

Metapopulation	<u>Managed/Unmanaged habitat patches</u>		
	Number	Mean size (ha)	Range (ha)
Cape Elizabeth	16/17	10.2/5.8	1.2-28.7/0.7-30.5
Kittery-Berwick	8/15	11.1/2.1	3.8-32.0/0.1-10.5

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 2). The most comprehensive data set (using multiple sites and years) on survival rates of NEC came from H. Kilpatrick (Connecticut Department of Energy and Environment, personal communication). Information on juvenile survival rates is lacking. We assumed juvenile rates to be equivalent to those of adults as reported in studies of other lagomorphs (e.g., Gillis Elizabeth 1998, Zeoli et al. 2008, Kielland et al. 2010). Using information on litter sizes from the NEC captive breeding program at the Roger Williams Zoo (L. Perrotti, Roger Williams Zoo, Providence, RI; unpublished report) and literature reports (summarized in Chapman and Litvaitis 2003), we estimated per capita recruitment as: per capita reproductive rate x annual survival rate (Akçakaya and Root 2013). Adult females averaged 2.5 litters with 4.17 young/litter, so per capita (male or female) recruitment would be $(2.5 \times 4.16)/2$ or $5.21 \times$ annual survival rate.

Table 2. *Estimated vital rates, carrying capacity, and dispersal distance 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)	0.13 (0.3)	H. Kilpatrick (pers. comm.), Brown and Litvaitis (1995), Villafuerte and Litvaitis (1996)
Annual survival rate on patches < 3 ha (sink populations)	0.065 (0.15)	H. Kilpatrick (pers. comm.), Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Carrying capacity	1 rabbit/0.5 ha	Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Recruitment per capita on patches ≥ 3 ha (source populations)	0.68 (0.22)	Chapman and Litvaitis (2003), L. Perrotti (unpublished report)
Recruitment per capita on patches < 3 ha (sink populations)	0.34 (0.11)	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)

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, we found that 1 in 10 winters had >100 days with snow on the ground. NEC mortality is strongly influenced by long winters (Brown and Litvaitis 1995), so our model included a 10% annual probability of a catastrophe (severe winter) in which 90% 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.

Environmental correlation is the concept that habitat patches close together will be similarly affected by events such as weather. NEC experience high environmental correlation (Villafuerte and Litvaitis 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 three scenarios (described below). For each scenario, we used a 15-year simulation that was replicated 1,000 times for both focus areas. 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 1,000 simulations for a specific management scenario that fell below a specific threshold of abundance.

Habitat Availability

Spatial information on unmanaged but suitable habitats was derived from known occupied habitat patches surveyed by Fenderson et al. (2014). Information on managed habitats was obtained 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. 4). For each patch included in our models, we

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.

Management Alternatives

We compared three management scenarios for each focus area.

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.

Current management: Managed patches are added to the unmanaged patches over time, but no maintenance is invoked so habitat abundance 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.

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 managed patches, if NEC habitat programs and funding continue for the foreseeable future.

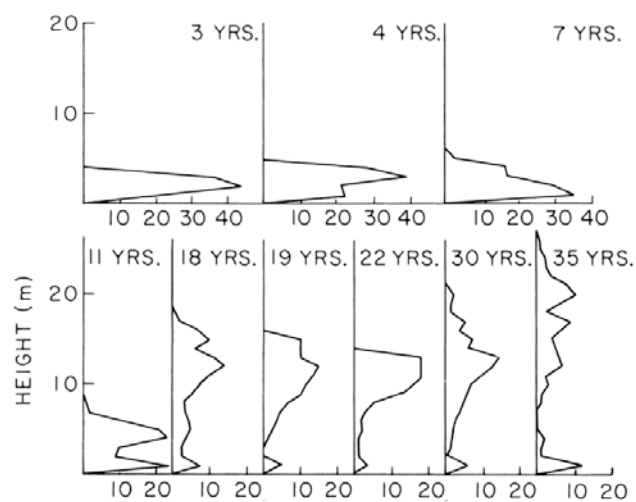


Figure 4. *Vegetation regeneration in a hardwood forest after a clearcut (from Aber 1979). By 18 years after management, the bulk of the vegetation is no longer in the understory and the habitat is unsuitable for NEC.*

Sensitivity Analysis

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). The values chosen were: mean survival and recruitment rates, standard deviations of the survival and recruitment rates, proportion of the population that disperses to another patch, and probability of an environmental catastrophe (severe winters).

RESULTS

Simulations

Overall abundance of NEC was higher in the maintained management scenario as compared to no management in both focus areas (Fig. 5 and 6). The current management scenario was generally higher than no management as well, but cottontail abundance declined during the 15-year projection. Similarly, the extinction risks were lower in the maintained management scenarios (Table 2). The Cape Elizabeth focus area had higher abundances and generally lower extinction risks than the Kittery-Berwick focus area.

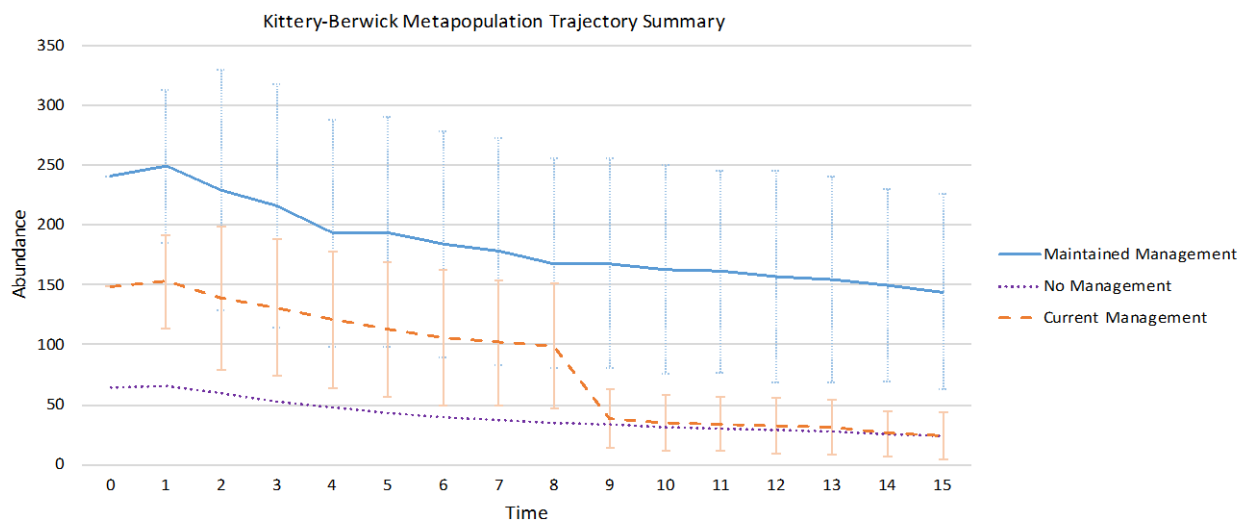


Figure 5. Average abundance (and standard deviations) of New England cottontail metapopulation in the Cape Elizabeth focus area in response to three management scenarios.

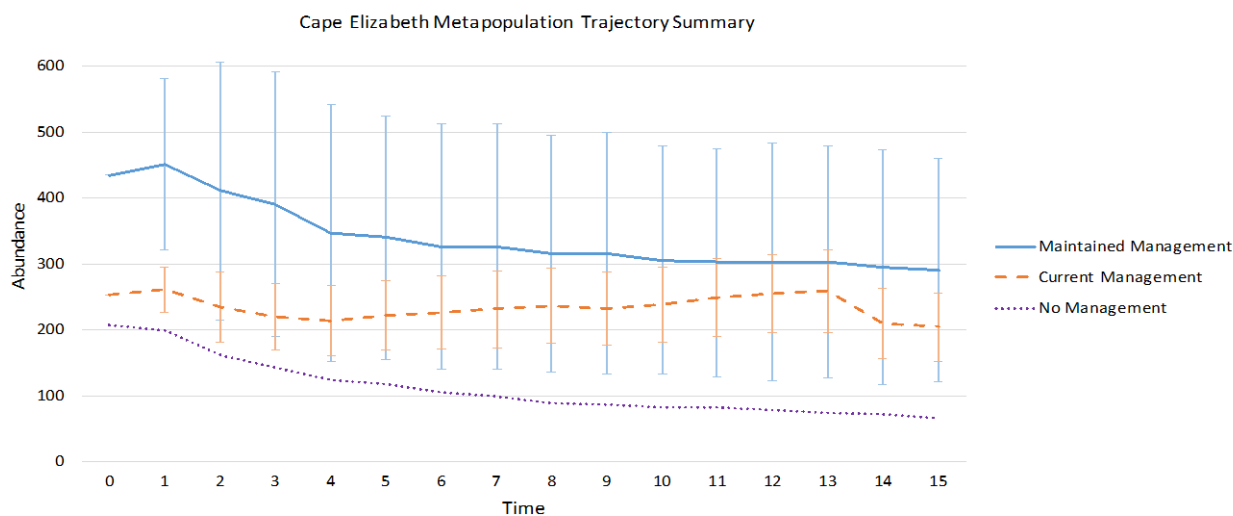


Figure 6. Average abundance (and standard deviations) of New England cottontail metapopulation in the Kittery-Berwick focus areas in response to three management scenarios.

Table 2. Probabilities of two New England cottontail metapopulations falling to specific abundance thresholds in response to three management actions.

Metapopulation	Action	Probability of reaching specific thresholds			
		200	100	50	0
Cape Elizabeth	No management	0.934	0.766	0.543	0.189
	Current management	0.488	0.011	0	0
	Maintained management	0.341	0.127	0.038	0
Kittery-Berwick	No management	1.000	0.998	0.883	0.079
	Current management	1.000	0.999	0.896	0.046
	Maintained management	0.766	0.347	0.111	0

Sensitivity Analysis

Altering mean survival and recruitment rates had little influence on the metapopulation extinction risks. However, increasing the variation (standard deviations) of these values and the probability of catastrophe (exceptionally snowy winter) had a substantial influence (Fig. 7). These results suggested that populations were more responsive to demographic and environmental variation than to changes mean vital rates and the proportion of dispersing individuals.

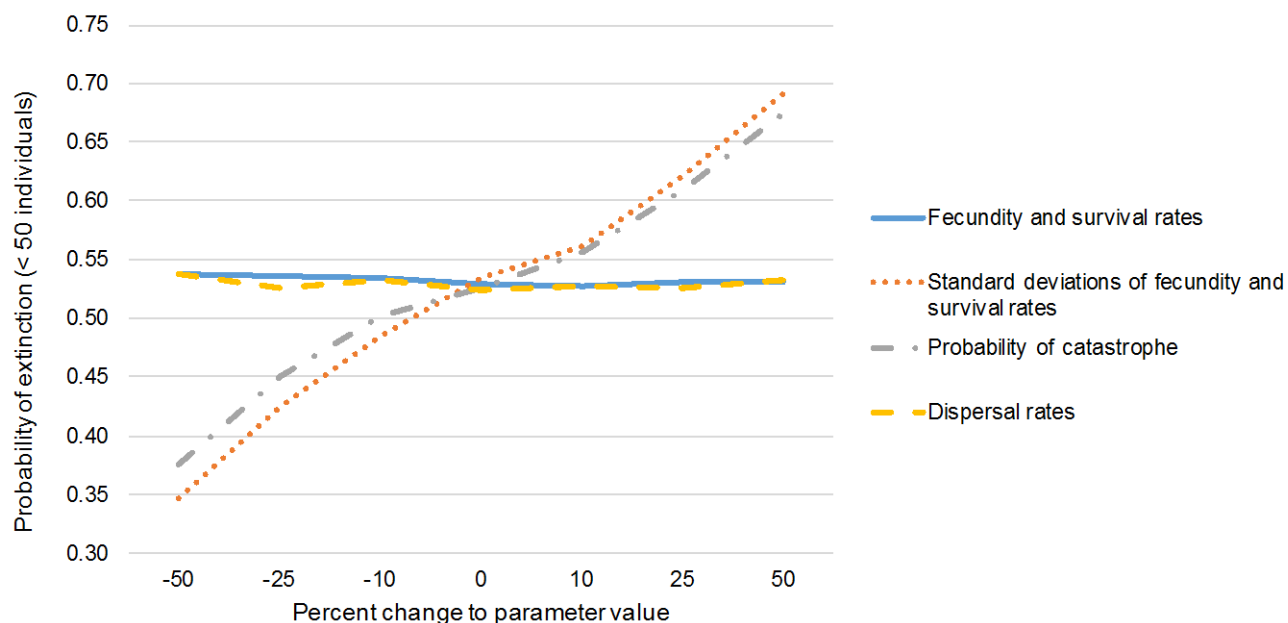


Figure 7. A sensitivity analysis of four model parameters: recruitment and survival rates, standard deviations of recruitment and survival rates, probability of catastrophe (representing severe winters), and dispersal rates (the proportion of the population that disperses to another patch).

MANAGEMENT IMPLICATIONS

Comparing the two focus areas was useful for evaluating how management activities may affect metapopulation growth and stability. The Kittery-Berwick is a larger area with fewer occupied habitat patches with few, large managed habitats. Based on our simulations, higher density of managed and unmanaged patches supported a greater abundance of NEC on Cape Elizabeth and with lower extinction risks, suggesting the focus area approach may be effective by placing habitat restoration efforts near occupied and other management sites. In both focus areas, there was reduction in extinction risk and an increase in abundance with the maintained management scenario because suitability declined on all patches with forest succession. Because NEC habitats lack regular forms of natural disturbance (e.g., fires) and suburban developments are likely to further reduce available habitats, management of habitats will need to continue to maintain these existing metapopulations.

The sensitivity analysis has implications for future research and habitat management. Because environmental and demographic variation (simulated by changes in the standard deviation associated

with parameters) and probability of a catastrophe were more influential than changes in average parameter values, monitoring of existing populations will be essential. However, factors affecting juvenile survival are unknown and may prove influential once identified.

Climate change studies indicate 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. Sensitivity analysis showed that the extinction risk of a metapopulation is highly sensitive to the probability of catastrophic mortality events (i.e., severe winters), as well as variation in annual survival and fecundity rates. As vital rates become more variable due to climate (meaning very high and low annual rates become more common), and as catastrophic mortalities become more probable, the risk of metapopulation extinction is higher. When a large percentage of the individuals in a metapopulation die, as is likely for NEC in a particularly long, snowy winter (Brown and Litvaitis 1995), it is less likely that the now-vacant patches will be re-colonized by neighboring populations. There may also be an increase in average winter temperatures, which could reduce the average number of days per year with snow, benefitting NEC somewhat; however, we hypothesize that NEC metapopulation extinction is influenced more by environmental variability and the frequency of severe snowy winters, that could increase with climate change, than by small increases to average survival rates. To mitigate that effect, populations of NEC and habitat should be closely monitored so that managers can intervene when needed by introducing captive bred rabbits to vacant patches and maintaining suitable habitat through management.

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Appendix A

Warren, A., J.A. Litvaitis, and D. Keirstead. 2016. Developing a habitat suitability index to guide management of New England cottontail habitats. *Wildlife Society Bulletin*. In Press.



Original Article

Developing a Habitat Suitability Index to Guide Restoration of New England Cottontail Habitats

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ABSTRACT Populations of taxa dependent on young forests and shrublands in the northeastern United States are declining in response to habitat loss and fragmentation. In particular, the reduction in distribution and abundance of the New England cottontail (*Sylvilagus transitionalis*; NECs) prompted consideration to list it as federally threatened or endangered. In response to those concerns, a range-wide conservation strategy for NECs has been developed that includes managing >20,000 ha of thicket habitats. Although much is known about the habitat associations of NECs, there is no obvious approach for evaluating the suitability of sites managed for them. We developed a habitat suitability model that conservationists can use to monitor progress in generating and maintaining habitats for NECs. We relied on literature reviews, expert opinions, and field data to identify habitat features that can be measured and indexed and used in a simple model to rank patches of habitat on a scale of 0 (unsuitable) to 1 (high suitability). Important features included dense understory vegetation, summer forage, and the presence-absence of additional refuges (e.g., constructed brush piles). We used our model to rank 60 managed habitats and found general agreement with opinions of an expert panel. There are obvious advantages to using a habitat-suitability model during efforts to restore populations of NECs: it provides a consistent approach for monitoring management actions, can be used to identify site-specific limitations prior to releasing cottontails in vacant habitats, and can be used to track suitability over time and alert managers of potential habitat deficiencies. Our suitability model also can be modified to accommodate new information and changing conditions. © 2015 The Wildlife Society.

KEY WORDS HSI, lagomorphs, restoration, *Sylvilagus transitionalis*.

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 [*Castor canadensis*] 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 U.S. Fish and Wildlife Service (USFWS) 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 historical 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 was made, several governmental (U.S. Fish and Wildlife Service, Natural Resources Conservation Service, and state fish and wildlife agencies within the current range of the NEC) and nongovernmental organizations (e.g., Environmental Defense Fund, National Fish and Wildlife Foundation, National Wild Turkey Federation, Wildlife Management Institute, and local land trusts) 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 enough to permit the U.S. Fish and Wildlife Service to forego listing NECs as threatened or endangered (USFWS 2015).

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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 are suitable for NECs.

Our approach was patterned after models developed by the 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 (max. 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 with 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 multistate 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 1) use literature reviews and expert opinions to identify variables that describe life requisites of NECs; 2) develop suitability indices for those variables that can be incorporated in a simple model to rank specific sites; and 3) 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 was in the northeastern United States, including the Hudson River Valley in New York, and portions of Connecticut, Massachusetts, Rhode Island, southeastern New Hampshire, and southwestern Maine (Fig. 1). In southern areas and along the Atlantic coast, forests were dominated by oaks (*Quercus* spp.) and pines (*Pinus* spp.). To the north, forest types included maples (*Acer* spp.), birches (*Betula* spp.), and American beech (*Fagus grandifolia*). Land uses varied throughout the region. In general, southern and coastal areas were characterized by a mix of urban-suburban

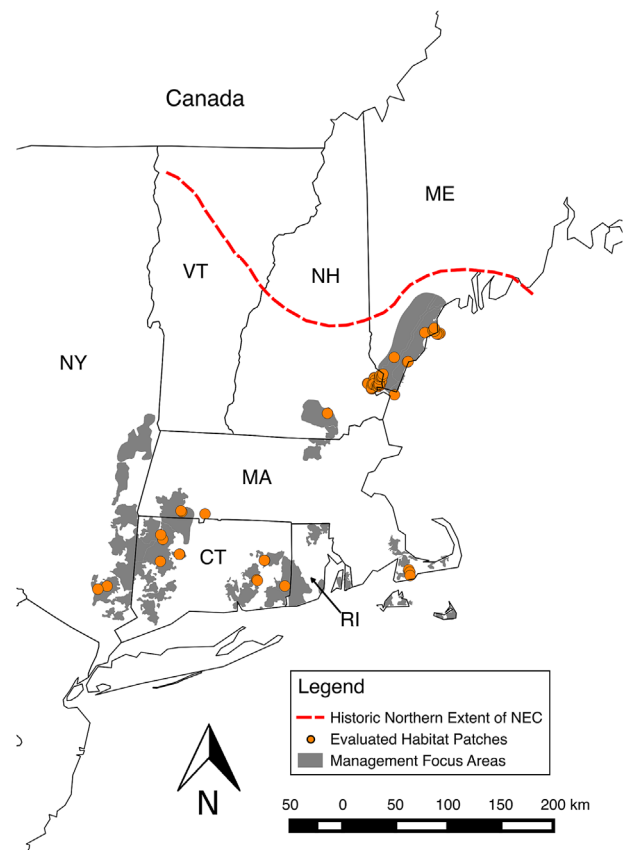


Figure 1. Current New England cottontail management focus areas and location of 60 managed sites within the eastern United States that were inventoried during development of a habitat suitability index.

developments, small woodlots, and scattered agricultural fields. Inland landscapes were dominated by large blocks of midsuccessional forests (Tash and Litvaitis 2007).

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 the 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 2007, Fenderson et al. 2011) 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.

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).

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 5 of the 6 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 × 1-m plots to inventory the woody understory vegetation (<7.5 cm diameter at breast height [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.

Table 1. Candidate variables of New England cottontail habitat based on literature review and majority opinion of their importance (ranked 1–4, 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 ht	Understory vegetation of a certain ht 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 interspersed index	Availability of forage near protective cover in summer.	Smith and Litvaitis (2000)	2
C ₉ : winter interspersed 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

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
V_1 : security cover	Percentage of the understory vegetation that has a density of >300,000 stem-cover units/ha. Includes C_{1+4} in Table 1.	Record understory-stem density by species in 10×1 -m plots and convert to stem-cover units (see text for details). Placement and no. 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, ≥ 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.
V_2 : other cover	Percentage of the understory vegetation that has a density of 100,000–300,000 stem-cover units/ha. Includes C_{2+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.
V_3 : ht of woody cover	Average ht of the understory vegetation in the patch (meters). Includes C_6 in Table 1.	Measure ht (m) of dominant understory vegetation in sample plots and calculate an average for the site.
V_4 : summer forage	Edge-to-area ratio of herbaceous openings to woody cover (m/ha). Includes C_{7+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 diam and determine length of edge (meters). Divide edge by area of managed site (ha). Verify the accuracy of the aerial photography in the field.
V_5 : additional refuges	Presence-absence of constructed brush piles, natural or artificial burrows, rock walls, and stone foundations. Includes C_5 in Table 1.	Suitable refuges noted as observed in the field.

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 (V_1) as the proportion of the patch with >300,000 stem-cover units/ha and other cover (V_2) 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; Google Inc., Googleplex, Mountain View, CA) were used to measure the length of grass-forb-shrub edges and the total patch area (V_4 ; Fig. 2).

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 1–5, 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 with 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.

Incorporating refuges (V_5) 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.

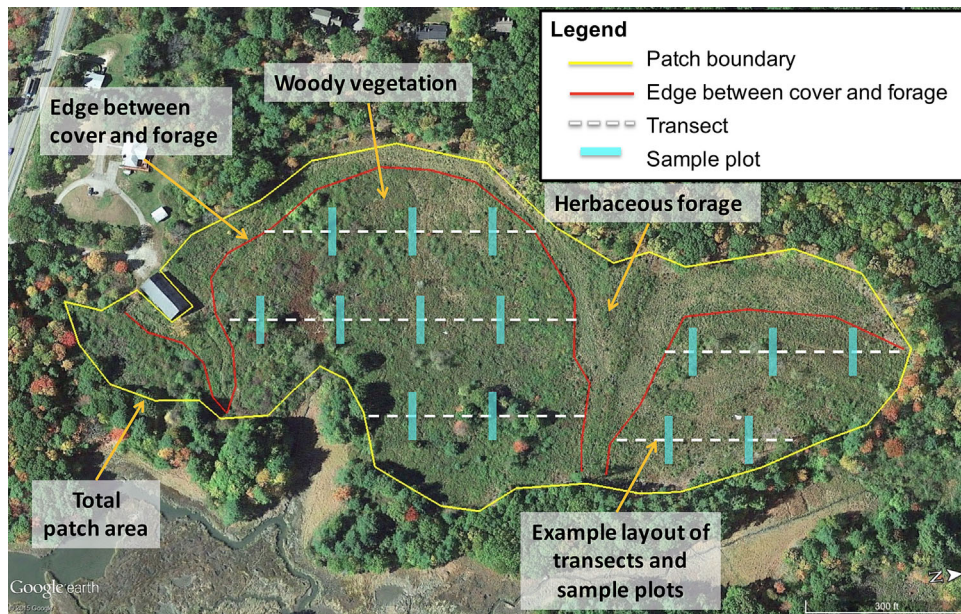


Figure 2. Example of an aerial photograph (from Google Earth; Google Inc., Googleplex, Mountain View, CA) used to measure patch area and summer forage availability (edge-to-area ratio of woody cover and herbaceous forage) at sites managed for the New England cottontails in the eastern United States. Also shown is an example of the sample plot layout for assessing habitat variables 1–3 used in the habitat suitability model.

Optimizing the Model

Following the USFWS protocol for developing a HSI model (USFWS 1981), we combined individual suitability indices into a function that produced a value of 0–1 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 5 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 and literature about the importance of each variable. We gave variables 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 we gave 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.

Optimized Model Structure

The final HSI model was a weighted average of 4 habitat variables plus the presence–absence of refuges (Eq. 1). Experts stressed the importance of dense vegetation (security cover) and

$$\text{HSI} = \frac{(3 \times V_1) + (2 \times V_2) + V_3 + V_4}{7} + V_5 \quad (1)$$

where,

V_1 = security cover

V_2 = other cover

V_3 = vegetation height

V_4 = summer forage

V_5 = refuges (addition of V_5 cannot result in the HSI exceeding 1.0)

Previous studies showed that NECs prefer dense 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 (V_1) a weight of 3 and other cover (V_2) a weight of 2. Height of woody vegetation (V_3), summer forage (V_4), and presence–absence of refuges (V_5) were considered 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

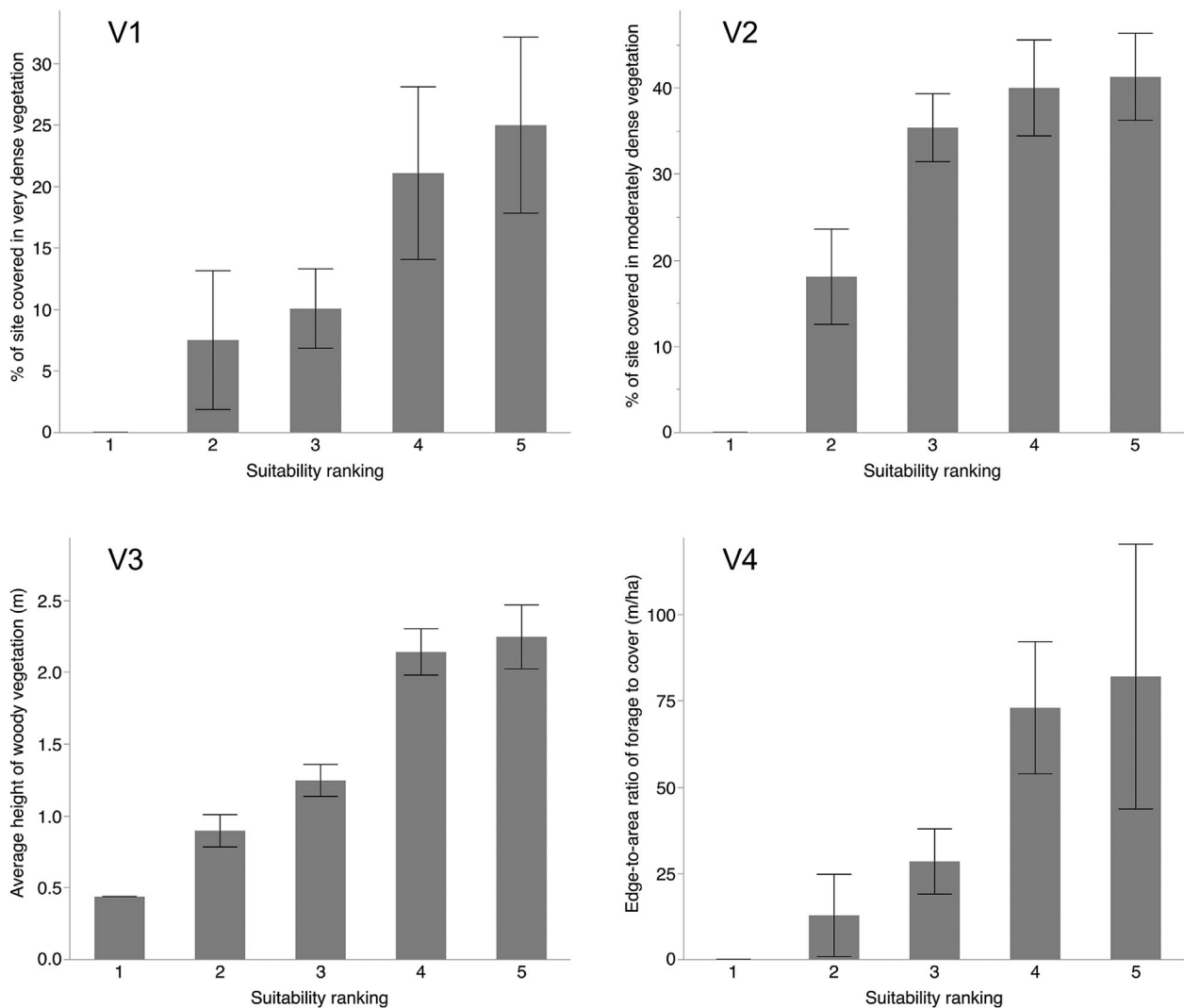


Figure 3. Average (and SEs) values of 4 habitat variables sampled among 60 sites in the eastern United States managed for New England cottontails; these variables were also ranked from 1 (not suitable) to 5 (highly suitable) by biologists knowledgeable on the requirements of New England cottontails.

(Fig. 5). Variability in the HSI score within each expert-opinion ranking category was expected. New England cottontails 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).

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 ($\mu = 0.67$, $SE = 0.05$) than for unoccupied sites ($\mu = 0.42$, $SE = 0.25$). Therefore, an initial threshold value for releasing rabbits on an unoccupied site could be an HSI score of 0.65–0.7.

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: $V_1 = 15\%$ coverage (SI = 0.58), $V_2 = 35\%$ coverage (SI = 0.58), $V_3 = 1.25$ m (SI = 0.63), $V_4 = 38$ m/ha (SI = 0.75), and $V_5 =$ Absent. Entered into our model, we generated a score just below the recommended threshold.

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

We could add brush piles (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 (V_1) and moderately dense (V_2) 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

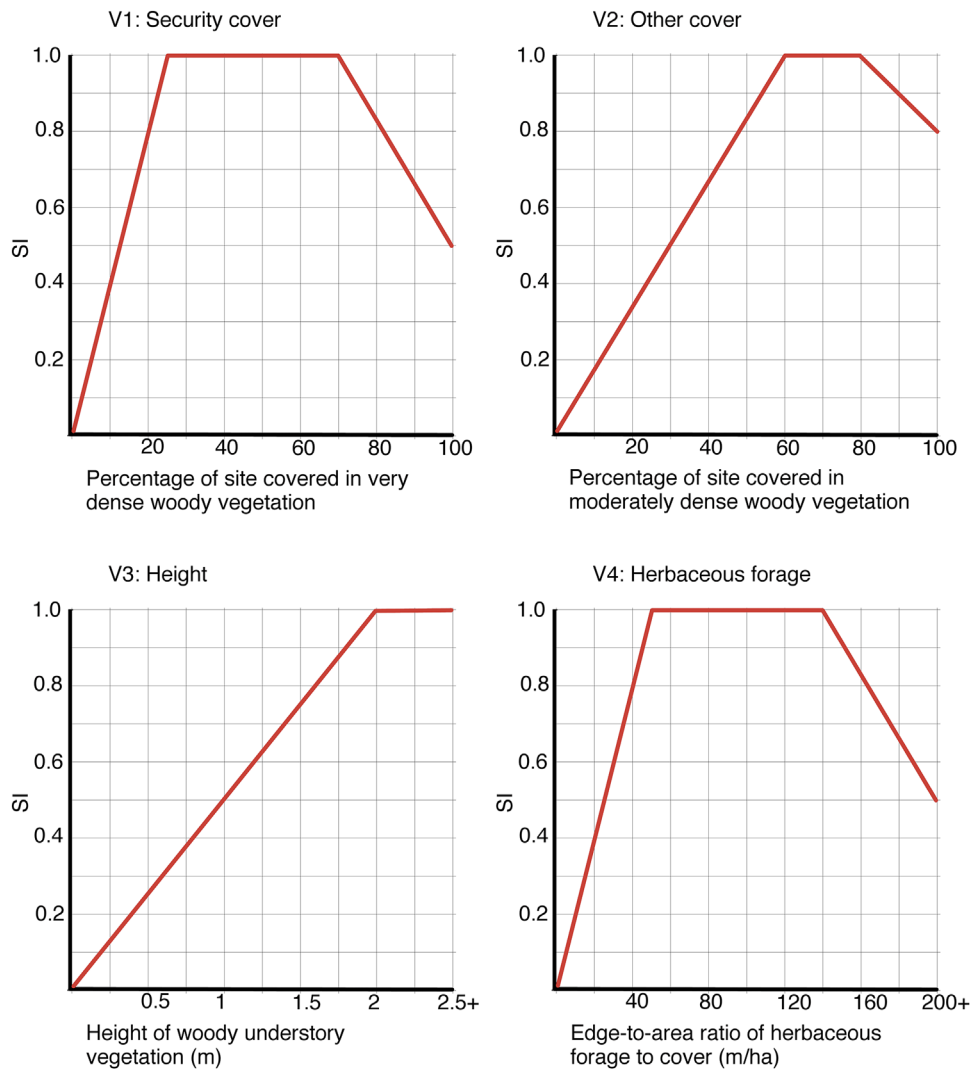


Figure 4. Suitability index (SI) curves for 4 habitat variables (V_1 – V_4) that describe life requisites of New England cottontails.

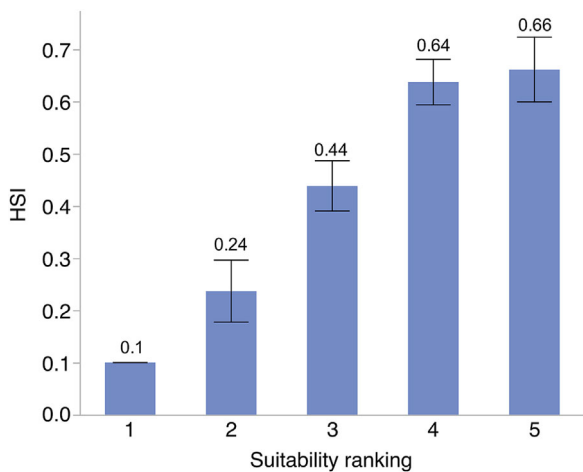


Figure 5. Average habitat suitability index (HSI) model scores (and SEs) for 60 sites in the eastern United States with expert-opinion rankings, where 1 was assigned to the least suitable sites and 5 was assigned to the most suitable sites for New England cottontails.

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 to, or even greater than, some native shrubs (Litvaitis et al. 2013); and relative value of

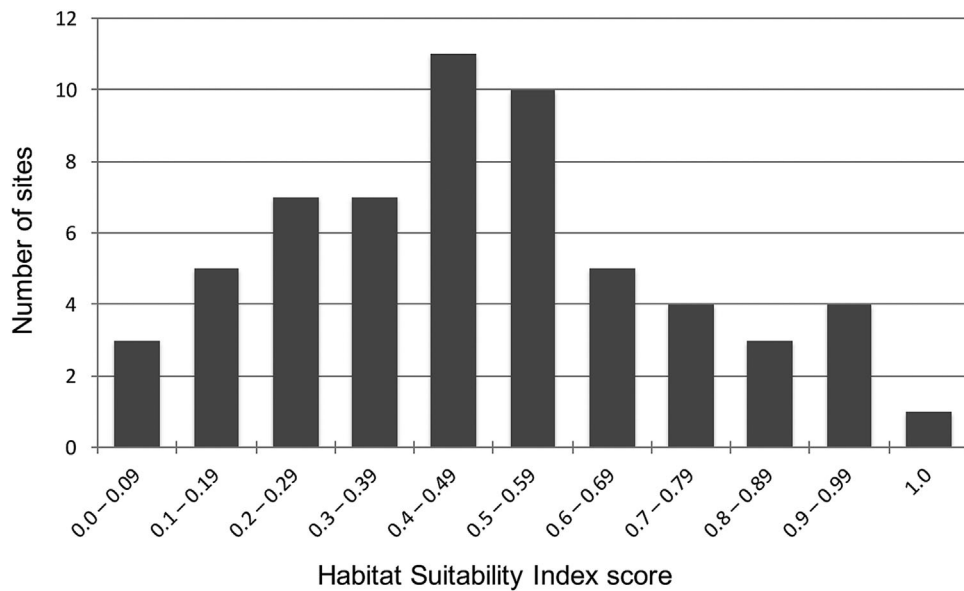


Figure 6. The distribution of habitat suitability index model scores for 60 sites managed for New England cottontails in the eastern United States.

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.

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APPENDIX A

Relative cover values of selected understory shrubs and young trees encountered on managed New England cottontail habitats. Values are based on the differences in visual obstruction among plants and were generated using a vegetation profile board. For example, dogwoods (*Cornus*) provide 4.28 times the cover as a raspberry (*Rubus*) stem. Data were collected in thicket habitats in New Hampshire and Maine in 2014.

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