

Monitoring habitat dynamics for rare and endangered species using satellite images and niche-based models

Rebecca A. Bartel and Joseph O. Sexton

R. A. Bartel (*rbartel@uga.edu*), Dept of Zoology, Box 7617, North Carolina State Univ., Raleigh, NC 27695-7617, USA, present address: Odum School of Ecology, Univ. of Georgia, Athens, GA 30602-2202, USA. – J. O. Sexton, Landscape Ecology Laboratory, Nicholas School of the Environment, Duke Univ., Durham, NC 27708-0328, USA.

The potential distribution of critically rare or endangered species is necessary to assess species conservation status and guide recovery plans. Habitat models based on remotely sensed geospatial data are increasingly used to predict the suitability of sites for rare and endangered species, but in rapidly changing landscapes, habitat evaluations must reflect temporal as well as spatial variation of environmental suitability in order to properly inform management. We used field measurements of species occurrence, a 22-yr time series of satellite images, and the Maximum Entropy modeling approach (Maxent) to monitor spatio-temporal variation in habitat suitability of an endangered butterfly that uses riparian wetlands modified by beaver activity. We modeled the niche of the St. Francis' satyr *Neonympha mitchellii francisci* in an environment of remotely sensed metrics and projected the niche model over space and time to evaluate habitat dynamics and target sites for reintroduction efforts. Suitable habitat for the subspecies is currently distributed across the study area; however, most of the suitable area is unoccupied, and patches of the most suitable habitat have shifted over time in response to beaver activity and subsequent wetland succession, suggesting a negative interaction between dispersal limitation and landscape dynamics. Landcover changes complicate the recovery of critically threatened species such as *N. m. francisci*, but habitat monitoring over time can improve recovery plans, offer adaptive management strategies, and provide more exact criteria for species status assignment. Spatio-temporal extensions of the niche/habitat concept are made possible by long-term archives of remotely sensed data, and will likely prove most useful in rapidly changing landscapes.

Knowledge of the potential distributions of critically rare or endangered species is necessary to designate and assess species listed under the U.S. Endangered Species Act (ESA) and subsequently to guide species recovery plans (Gerber and Hatch 2002, Hoekstra et al. 2002). However, because of the pressing need to evaluate the distribution of endangered species for conservation planning, long-term population studies are often not feasible. Alternatively, management decisions can be informed by statistical models based on environmental determinants of a species' distribution (Guisan et al. 2006).

Species distribution models approximate a species' environmental niche (Hutchinson 1957), which is then projected geographically to produce habitat maps (Hutchinson 1967, Guisan and Zimmerman 2000). Bridging the gap between science and management, habitat modeling both describes the environmental requirements of species and uses this information to target conservation and recovery efforts (Elith et al. 2006, Phillips et al. 2006). Improvements in predictive algorithms and geospatial databases have increased the reliability of habitat models for rare and endangered species recovery (Guisan and

Thuiller 2005, Guisan et al. 2006), but most applications rely upon habitat maps for only a single snapshot of time. This can be problematic where succession or other landcover changes alter the distribution of suitable sites over time.

Defining the appropriate spatial and temporal scales of habitat models is complicated. Habitat models assume that the spatial distribution of a species reflects its environmental niche requirements (Kearney 2006), but effectively capturing all suitable sites can be difficult in practice (Guisan and Thuiller 2005, Early et al. 2008). Distributions of critically rare and endangered species are often reduced or restricted (Gaston 1994); as a result it is difficult to discriminate unsuitable habitat from merely unoccupied habitat (Davis et al. 2007). To assess whether unoccupied sites may indeed be suitable, it is necessary to differentiate between environmental factors and landscape constraints on habitat suitability (Talley et al. 2007). Estimating the suitability of unoccupied habitat is essential to designating critical habitat, predicting future distributions, planning conservation strategies, and avoiding incorrectly listing or delisting threatened or endangered species (Doremus and Pagel

2001); yet this information is often missing from species recovery plans (Hoekstra et al. 2002).

We show how habitat models can predict the potential distribution of rare species over time to guide recovery efforts. As a case study, we use a large spatio-temporal dataset to assess habitat suitability for the endangered St. Francis' satyr *Neonympha mitchellii francisci* butterfly and monitor habitat changes over two decades. We use a 22-yr series of geometrically and atmospherically corrected Landsat Thematic Mapper (TM) satellite images, in-situ species occurrence data, and the Maximum Entropy modeling approach (Phillips et al. 2006) to produce a spatiotemporal habitat map for a species with specific and localized environmental requirements. After validating habitat extrapolations on an independent data set of known butterfly presences and absences collected through field surveys, we monitored temporal changes in habitat over the study area and used the projections to target sites for reintroduction efforts.

Methods

Study area

Neonympha mitchellii francisci are known only to exist in south central North Carolina (USA), on Ft. Bragg military reservation (35°07'30"N, 79°08'30"W), located on Dept of Defense lands within the Sandhills region of the Inner Coastal Plain physiographic province. Ft. Bragg was created in 1918 and is currently an active army base covering ca 65 032 ha.

Total population estimates of *N. m. francisci* range between 700 and 1400 adult individuals for all accessible areas (Kuefler et al. 2008) that are not within military artillery zones. The butterflies occur in several subpopulations in early successional riparian vegetation containing their presumed host plants. Although *N. m. francisci* caterpillars have never been observed in nature, previous feeding experiments and field surveys (Kuefler et al. 2008) suggest that the primary larval host plant of *N. m. francisci* is *Carex mitchelliana* in addition to other *Carex* species. Multiple subpopulations comprise a metapopulation in a single watershed, and a network of watersheds connects the rangewide population (Kuefler et al. 2008). These wetlands are created and maintained by beaver *Castor canadensis* through dam-building and the resulting flooding and initiation of vegetative succession (Bartel 2008). Natural and managed fires are common in the surrounding upland forests and occasionally spread into wetlands.

Presence/absence data

During the study period, there have been 23 known *N. m. francisci* subpopulations scattered across the stream network on Ft. Bragg. Fourteen of these subpopulations occupy five different watersheds within inaccessible military training areas, where activities such as munitions testing preclude habitat surveys. Six of the nine accessible subpopulations currently maintain active butterfly colonies (Kuefler et al. 2008). Field surveys began in 1992 and were opportunistic until 2002, at which time regular habitat and population

surveys began in the active subpopulations on three watersheds. These efforts are ongoing and also include monitoring transitory and previously occupied areas across the entire accessible area of the base for new butterfly occurrences.

To create a spatial data layer for butterfly presence, we first compiled all known areas with a history of butterfly presence. In 2005, a survey of stream channels and adjacent wetlands delineated patches of habitat containing *N. m. francisci* with a global positioning system (GPS). These polygons were then checked on orthorectified, 1-foot resolution color images taken in 2006, and points representing suitable habitat were placed in and around the polygons. Each GPS polygon was then modified by drawing a refined polygon around its photo-interpreted points. In 2007, surveys were conducted to record *N. m. francisci* presence in some previously restricted areas, in addition to regularly monitored wetlands.

To create the corresponding spatial data layer of *N. m. francisci* absence for the wetlands surveyed in 2007, the surveyed wetlands were identified in the National Wetlands Inventory (NWI) shapefile (<www.fws.gov/nwi/>) and areas within the refined "presence" polygons were removed from the dataset. Thus, all surveyed NWI wetlands without *N. m. francisci* presence recorded for 2007 were treated as absences. To record *N. m. francisci* absences in uplands, 146 points were digitized on aerial images in upland patches within drainages in which *N. m. francisci* presences were recorded during the 2007 survey. The upland absence points and wetland presence and absence polygons were used to extract values from the satellite images; all pixels within wetland polygons and a single pixel from each upland point were collected for a total sample of 223 (wetland) presences, 4687 wetland absences, and 146 upland absences.

Environmental indices

Six summer (May) and six winter (December–January) approximately anniversary-dated Landsat-5 Thematic Mapper (TM) images taken from 1985 to 2007 (Table 1) were rectified to a mosaic of 1-m resolution orthorectified digital aerial photographs. Geometric root mean-squared error of independent test points ranged from 15.4 to 28.3 m. After rectification, images were converted to radiance (Chander et al. 2007) and then to estimates of surface reflectance using the DOS3 approach (Song et al. 2001). The images were clipped to the boundary of Ft. Bragg, and clouds and snow were removed using a mix of on-screen digitizing and unsupervised classification. The geometrically, radiometrically, and atmospherically corrected surface reflectances were then transformed to Tasseled-Cap "brightness", "greenness", and "wetness" indices (Kauth and Thomas 1976, Crist and Cicone 1984) using coefficients calibrated for Landsat TM-5 surface reflectances (Crist 1985). These three metrics are linked closely to soil and vegetation properties: dominated by soil and vegetation albedo in the visible wavelengths, brightness is influenced by vegetation type and structure; greenness responds to vegetation cover and photosynthetic capacity (Cohen and Goward 2004); and wetness responds to standing water and soil/canopy moisture. These metrics have recently been successfully

Table 1. Landsat-5 Thematic Mapper imagery time series.

Year	Use	Summer date	Winter date
1985	Extrapolation	1 May, 1985	12 January, 1986
1986	Extrapolation	4 May, 1986	30 December, 1986
1989	Extrapolation	28 May, 1989	9 December, 1990
1993	Extrapolation, validation	23 May, 1993	1 December, 1993
1997	Extrapolation, validation	18 May, 1997	28 December, 1997
2007	Calibration, extrapolation, validation	14 May, 2007	5 December, 2006

applied to species distribution models (Zimmermann et al. 2007). Brightness, greenness, and wetness pixels were extracted from wetlands surveyed in 2007. We evaluated relationships between indices by comparing Pearson correlation coefficients across the wetland sample (SAS Inst. 2004). As a final check for within-season phenological artifacts, distributions of indices within and among image-dates were plotted over time and compared for trends.

Niche models

The extreme rarity of *N. m. francisci* suggests that many environmentally suitable locations are not occupied due to host plant distribution, competition, dispersal limitation, historical legacy, or other factors (Pulliam 2000). Such a prevalence of external factors could lead to indeterminacy and poor resolution of habitat models (Sexton et al. 2006). We therefore applied two methods with different treatments of observed absences to evaluate the efficacy of habitat models based on presence and absence data versus models built on presence data alone. These different treatments of absences lead to different interpretations of model estimates: models using both presence and absence data predict probability of presence, whereas models using presence data only predict a more general index of environmental suitability (Elith et al. 2006, Phillips et al. 2006).

Classification and regression trees. We fit classification and regression tree (CART) models (Breiman et al. 1984) using presence and absence data to model the probability of butterfly presence. The CART algorithm recursively partitions the environmental domain to maximize homogeneity of the response variable (i.e. presence vs absence) within the partitioned subsets. The process repeats for each subgroup, splitting samples into groups using the difference between each of two levels of the predictor variable as a threshold value. This procedure continues until a stopping rule is met or when the groups are too small to divide further (Vayssières et al. 2000).

We fit an initial classification tree of *N. m. francisci* presence/absence over summer and winter Tasseled Cap brightness, greenness, and wetness using the tree package in the R statistical computing language (R Development Core Team 2007, Ripley 2007). To avoid model over-fitting, we pruned the initial tree by setting model complexity to the number of splits at which residual deviance was minimized in cross-validation tests. We assessed model fit by cross-validation and examined both the overall misclassification rate and a confusion matrix of 2007 presences and absences.

Maxent. We estimated butterfly habitat suitability based on presences observed in 2007 and summer and winter

Tasseled Cap brightness, greenness, and wetness from 2007 using the Maximum Entropy modeling approach, via the Maxent software, ver. 3.1 (Phillips et al. 2006, Phillips and Dudík 2008). The Maximum Entropy algorithm estimates the realized niche by finding the probability distribution of species presence that is most spread-out (i.e. closest to uniform), constrained by the data relating presence to the environment (Phillips et al. 2006). Specifically, the fit is constrained using a set of features (real-valued functions, e.g. linear, quadratic, “hinge”, and “threshold”) such that the mean of each raw or transformed environmental variable under the estimated distribution must equal the same mean under the measured data, within tolerances set by a regularization parameter (Dudík et al. 2004). Maxent does not require absence data points for the modeled distribution. Instead, the probability distribution is defined only on species presences, extrapolating the distribution to all the pixels of the study area, termed the “background” (Phillips et al. 2006). The Maxent approach shares many advantages with CART, including: 1) the ability to use both continuous and categorical data, 2) modeling of interactions between variables, 3) the use of efficient numerical algorithms to converge on an optimal probability distribution, and 4) continuous output which allows for distinguishing the modeled suitability of different areas (Phillips et al. 2006). In addition to predicting habitat suitability for rare species (Davis et al. 2007, Pearson et al. 2007), Maxent models have been used to evaluate effects of invasive species (Ward 2007, Giovanelli et al. 2008) and climate change (Hijmans and Graham 2006) on species’ distributions.

We randomly selected 80% of the 2007 presence points ($n = 176$) as training data, with the remaining data ($n = 47$) reserved for testing the model results. Default settings were used for the convergence threshold (0.00001), maximum iterations (1000), and background points (10 000), but the default regularization multiplier ($r = 1$) was doubled as a conservative measure to avoid model over-fitting.

After fitting the Maxent model, we applied it to summer/winter pairs of Tasseled Cap images from 1985, 1986, 1989, 1993, 1997, and 2007 to extrapolate habitat suitability over time. For each of these years, we mapped the continuous suitability index and also “prime” habitat, identified by thresholding suitability above a cutoff value. Maxent calculates and reports several thresholds based on different optimality criteria. Preliminary results showed that interpretation of habitat maps was facilitated by imposing a more stringent threshold on the suitability maps than those provided by Maxent. We therefore defined “prime” habitat as locations with suitability greater than twice the value of the strictest threshold reported, which in this case was the logistic suitability value at which model sensitivity equaled specificity in the 2007 test dataset.

We applied several techniques to evaluate the Maxent model. First, we used a jackknife test of variable importance to compare models with all combinations of the environmental variables. We then plotted the receiver operating characteristic (ROC) curve, which differentiates model performance at all possible thresholds by a single number, the area under the curve (AUC). ROC curves plot sensitivity against (1 – specificity), where sensitivity is the proportion of observed presences correctly predicted and (1 – specificity) is the proportion of absences incorrectly predicted. Because this omission test is highly sensitive to the proportional predicted area, it cannot be used to compare Maxent model performance directly (Anderson et al. 2003, Phillips et al. 2006). To allow direct comparison, Maxent uses an equalized predicted area test that selects thresholds that result in binary models with the same predicted area (Phillips et al. 2006). Maxent uses an adapted ROC curve that is defined by plotting model sensitivity (1 – omission rate) over specificity (1 – fractional predicted area) (Phillips et al. 2006) across the [0, 1] range of possible thresholds. Last, we validated model extrapolations on an independent data set of observed *N. m. francisci* presences for 1993 and both presences and absences for 1997 and 2007, calculating and comparing confusion matrices from these years to those of the 2007 predictions. Because absences were defined as patches in which *N. m. francisci* had been observed over the course of the study but were not occupied in 1997, this validation provided the strictest possible examination of specificity.

To monitor changes in habitat suitability over the 22-yr study period, we compared the area-weighted logistic habitat suitability indices and prime habitat areas for the study area, plotting these values as a time series. To examine spatial patterns of habitat gain and loss, we mapped the difference between the 1986 and the 2007 suitability extrapolations. We excluded the 1985 image due to scattered clouds, which had been recoded to missing values in the cloud-removal process.

In order to rank sites for butterfly relocation and reintroduction, we defined a series of rules to maximize the likelihood of butterfly survival based on habitat suitability, trends over time, and the logistics of managing endangered species on an active military base. Specifically, reintroduction should be focused on areas of: 1) prime habitat value, 2) area > 0.2 ha, and 3) increasing habitat suitability. Patches selected for reintroductions should also be located: 4) outside restricted military activity zones to avoid conflicting uses and 5) within NWI-delineated wetlands to maximize legal protection. We chose the area constraint based on observations of butterfly subpopulations that were unable to persist given smaller patches of habitat (N. Haddad pers. comm.).

We encoded these rules in a set-theoretic site selection index (SSI):

$$SSI = PRIME \cap AREA \cap INC \cap \neg MAZ \cap NWI, \quad (1)$$

in which “PRIME” is prime habitat value, “AREA” is whether the pixel is part of a patch > 0.2 ha in size, “INC” is increase in habitat suitability between 1986 and 2007, “ \neg MAZ” is whether the pixel is not within a military activity zone, and “NWI” is whether the pixel lies within an NWI polygon. To accommodate the continuous nature of

INC with the other binary variables, we used fuzzy logic (Roberts 1986), which translates eq. (1) to:

$$SSI(x) = \min(PRIME(x), AREA(x), INC(x), 1 - MAZ(x), NWI(x)) \quad (2)$$

for each pixel (x) of the study area.

Results

Presence/absence data

NWI-delineated wetlands occupy 4337.22 ha, or 6.94% of Ft. Bragg. Within these wetlands, *N. m. francisci* were observed in 18.34 ha during at least one survey from 1992 to 2007. They were detected in 11.93 ha outside of NWI wetlands. *Neonympha mitchellii francisci* were observed in 8.16 ha of NWI wetlands in 1993 and 1.55 ha in 1997. Of the 10 patches (7.17 ha of wetland) occupied in 2007, five areas in 1993 and two areas in 1997 were also visited and confirmed as occupied.

Environmental indices

Within seasonal windows, spatial variation exceeded temporal variation of Tasseled-Cap bands (Supplementary material Fig. S1), suggesting minimal phenological noise and strong potential for model extrapolation across image dates. Standard deviations of within-scene average brightness, greenness, and wetness were, respectively, 0.010, 0.016, and 0.011 for summer images and 0.012, 0.006, and 0.008 for winter images. In comparison, seasonal averages of within-scene standard deviations of brightness, greenness, and wetness were 0.045, 0.042, 0.027 for summer images and 0.036, 0.029, and 0.027 for winter images. The average ratio of temporal to spatial standard deviation was 2.83 for summer Tasseled-Cap bands and 3.55 for winter Tasseled-Cap bands. The detection of more intra-scene variability vs inter-scene variability indicates the stability in the images and allows extrapolation across image years.

We compared correlation coefficients for all environmental indices, but only present statistically significant results with Pearson correlation coefficients > 0.5. Summer brightness was positively correlated to winter brightness ($r = 0.679$, $p < 0.001$) and negatively related to both summer and winter wetness ($r = -0.697$, $p < 0.001$; $r = -0.595$, $p < 0.001$). Winter brightness was negatively associated with winter wetness ($r = -0.662$, $p < 0.001$). Summer and winter wetness were also strongly correlated ($r = 0.563$, $p < 0.001$).

Niche models

CART. CART models showed that high winter wetness (> -0.057) and high summer greenness (> 0.222) predicted butterfly presence most effectively. The pruned tree had a residual mean deviance of 0.347 and misclassification rate of 0.04. However, the model fit was dominated by *N. m. francisci* absences: the model misclassified three of 4833 absences as habitat versus 216 of 223 presences as

non-habitat. Given the low sensitivity of the CART models (0.03), we discontinued further evaluation using CART techniques.

Maxent. The jackknife analysis of variable importance showed most variables contributed equally to the models, indicating there was enough pattern in the data that one variable could be removed and replaced by the another. The exception to this was winter greenness, which contributed little to the model (Fig. 1a). Both training and test AUC values were better than random, 0.898 for the training sample and 0.876 for the test sample (Fig. 1b), suggesting little model over-fitting. Based on the equal training sensitivity and specificity threshold (0.356), the Maxent model correctly classified 9 of 10 presences (sensitivity = 0.900) and 16 of 18 absences (specificity = 0.889), for a total classification accuracy of 89.29% in the model training year 2007. In the validation years, Maxent correctly classified 8 of 9 presences (sensitivity = 0.889) in 1993, and 2 of 2 presences (sensitivity = 1.0) and 0 of 3 absences in 1997.

Habitat suitability corresponded to the stream network and riparian zones of the study area (Fig. 2a). Prime habitat patches were located in wetlands on stream channels in small, frequently isolated patches (Fig. 2a). The area covered by prime habitat doubled from 1986 to 2007 (Fig. 3), ranging from 1.2% of the study area (718.02 ha) in

1989 to 2.5% (1534.41 ha) in 2007. In contrast, predicted suitability-weighted area increased sigmoidally over the study period, rising slowly from a minimum of 6133.01 ha in 1985, sharply through an inflection period between 1989 and 1993, and slowly again to a maximum of 11 250.54 ha in 2007. This increase in habitat suitability over time was statistically significant ($p = 0.016$, $r^2 = 0.804$), with the largest increase during 1989–1993 (Fig. 3). While values of prime habitat suitability were higher in 2007 than in 1985, there was less evidence of an overall increasing trend in 2007. Change in suitability closely followed a topographic gradient: increases were located in wetlands and riparian areas, whereas decreases were restricted to uplands (Fig. 2b).

Neonympha mitchellii francisci reintroduction potential currently varies from zero (i.e. not suitable) to 0.50. Among positively (nonzero) valued sites, the mean and standard deviation across Ft. Bragg are 0.17 and 0.08. Suitable sites are scattered across the riparian zones of Ft. Bragg, but two locations show special promise due to large, contiguous patches with high reintroduction potential (Fig. 4). Reintroduction potential is variable within these patches (Fig. 4, insets); since the increase in suitability from 1986–2007 was the only continuous criterion in the site suitability index, the fine-scale variation is in response to temporal changes in environmental suitability.

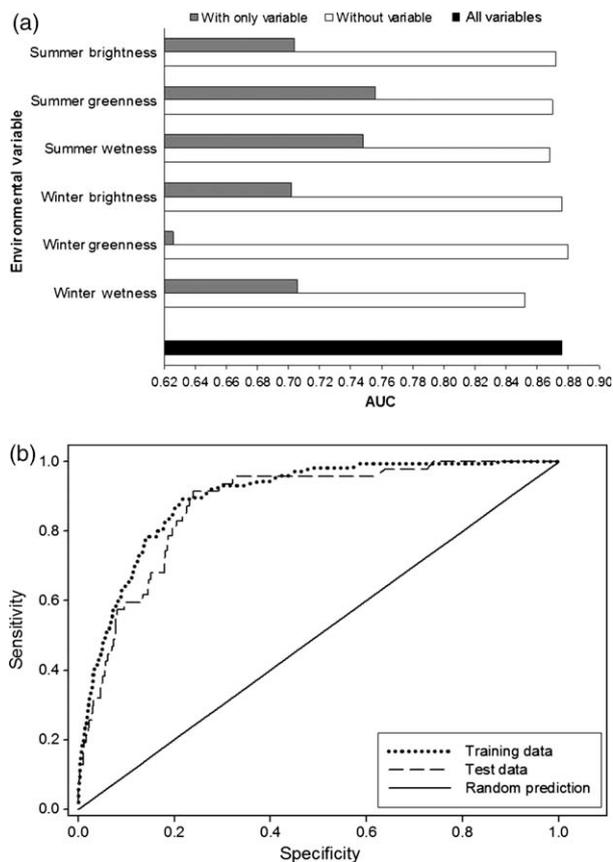


Figure 1. Results from Maxent models: (a) jackknife test of variable importance for test sample and (b) receiver operating characteristic (ROC) curve and calculated the area under the curve (AUC) metric.

Discussion

Rare species, by definition, have restricted spatial distributions (Gaston 1994, Hernandez et al. 2006), and their absences are often uninformative of their environmental requirements (Elith et al. 2006, Phillips et al. 2006) because individuals do not occupy all available habitat (Hirzel et al. 2001) and may be difficult to detect in occupied but inaccessible sites (Engler et al. 2004). By isolating the niche relationships in occurrence data, presence-only habitat models supply knowledge of species' environmental and spatial distributions with less dependence on spatial and observational factors (Elith et al. 2006). Numerous recent studies have successfully applied niche-based models using presence-only data to map habitat in space (Phillips et al. 2006, Pearson et al. 2007). Using a case study of the endangered Saint Francis' satyr butterfly *N. m. francisci* we found that the presence-only habitat modeling approach can be further applied to monitor habitat changes over time; an approach that is especially useful in dynamic landscapes where successional or other landcover changes drive patterns of habitat suitability.

Dynamic habitat maps in rare species conservation

Niche-based habitat models guide rare species monitoring, conservation, and restoration (Guisan et al. 2006, Early et al. 2008) and have even resulted in the discovery of new species in remote areas (Raxworthy et al. 2003). In the case presented here, a critically endangered subspecies occupies habitat within inaccessible areas of military activity. Opportunities to investigate these sites are extremely rare, but predictive habitat maps can increase search efficiency

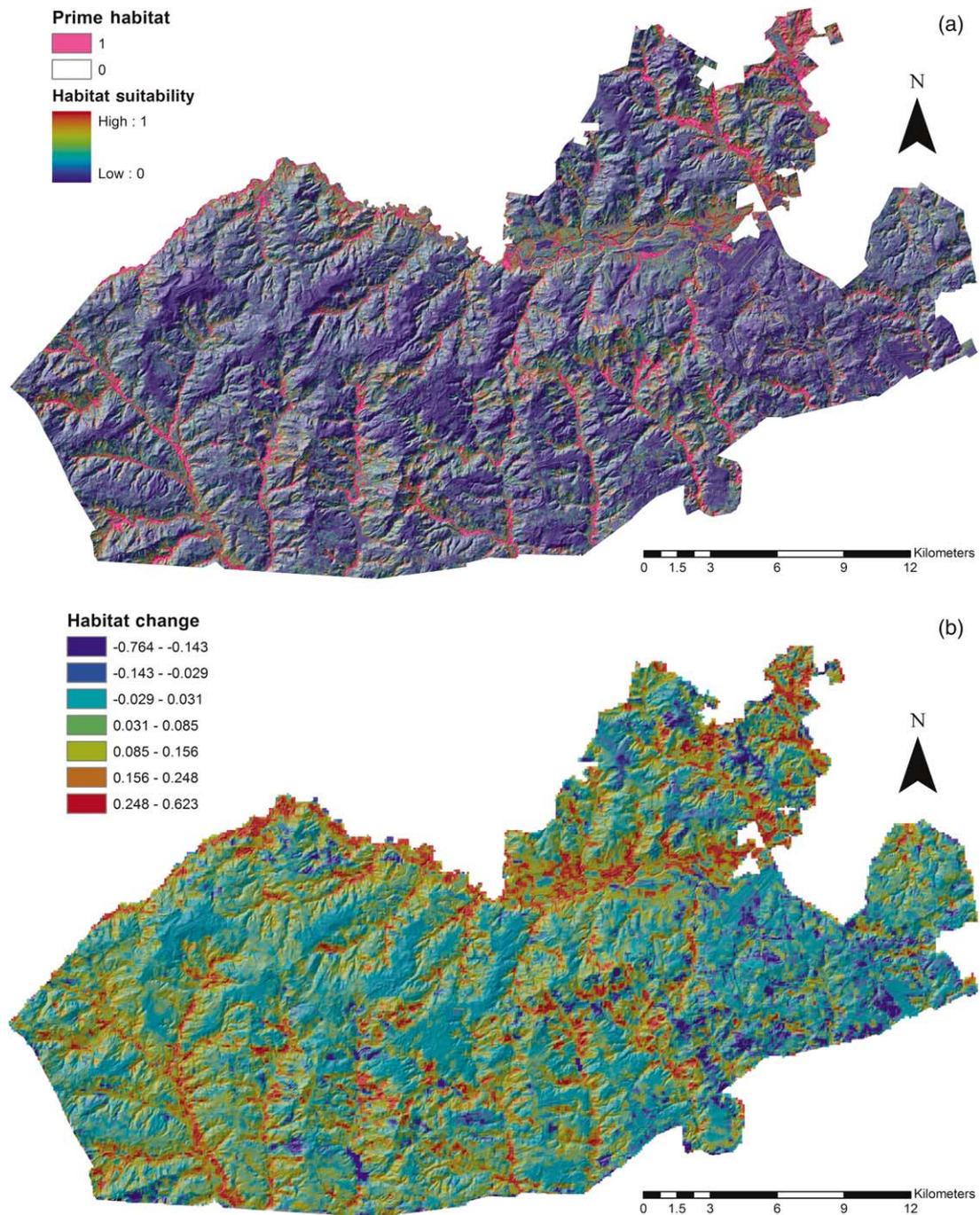


Figure 2. Predicted potential habitat suitability in 2007 by Maxent for (a) total and prime areas of butterfly habitat and (b) changes in habitat suitability from 1986 to 2007.

when opportunities for site surveys are granted, increasing the likelihood of encountering new subpopulations on the base. More broadly, wetlands of the southeastern United States are inaccessible simply due to their difficulty of traversal, so broader spatial extrapolation of habitat models may locate entirely new subpopulations of *N. m. francisci* to further assist region-wide recovery efforts.

Over time, monitoring and modeling comprise a feedback system (Urban 2002), co-adapting toward the goal of precisely locating sites for management action (Sexton et al.

2006). Guided by versions of the model extrapolated on updated satellite data, surveys for *N. m. francisci* will expand into previously unexamined locations. In return, on-site monitoring of *N. m. francisci* occurrence will provide data and immensely valuable field expertise to refine the model. The habitat model presented here initiates the recursion by providing a spatially explicit hypothesis to be tested by further validation and eventual *N. m. francisci* reintroduction. Additional field investigation will address how to better distinguish what is suitable habitat for this rare

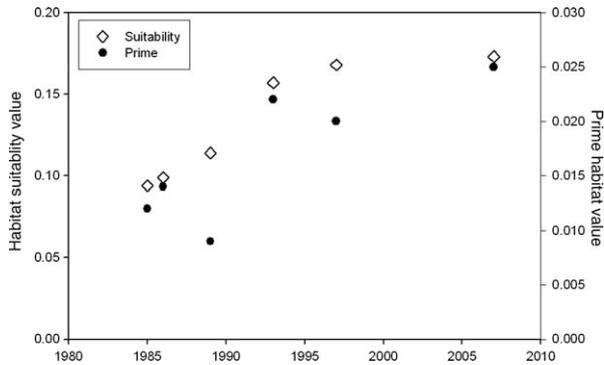


Figure 3. Changes in habitat suitability and prime habitat area for the study area 1985–2007.

species, allowing more precise identification of prime habitat and explain the unoccupied areas of predicted high quality habitat for *N. m. francisci*. Potential modeling improvements include incorporation of topographic variables to better isolate wetlands (Barling et al. 1994) and modeling errors from remote sensing, niche estimation, and GIS overlay operations (Arbia et al. 1998).

In addition to their well-established spatial utility, habitat maps projected over time can better inform management decisions and advance ecological theory. Metapopulation theory assumes that populations persist through colonization and extinction of subpopulations,

implying that species distributions vary in time even while the distribution of habitat does not (Early et al. 2008). Our results further show that the underlying habitat is itself variable and can lead to local extirpation and isolation of subpopulations. By combining knowledge of known occurrences with robust environmental factors or “direct environmental gradients” (Austin 1980), habitat models can inform predictions and site selection algorithms beyond the spatial and temporal domains over which they were fit. Unlike simple snapshots of habitat pattern, these spatio-temporal extensions of habitat suitability can assist successful reserve design by addressing impacts of habitat loss and fragmentation while forecasting long-term patterns of persistence (Cabeza and Moilanen 2003).

To manage species effectively, long-term species’ occurrence data must be matched by long-term data relating to environmental changes (Early et al. 2008). Our findings confirm that habitat models can be used to monitor landscape dynamics over time, focusing specifically on changes pertaining to a species’ environmental niche. In habitat modeling, occurrence data is assumed to be drawn from source habitat (Phillips et al. 2006), yet changes in either environmental suitability or landscape structure may affect these dynamics and ultimately influence metapopulation persistence (Hanski and Gaggiotti 2004). Basing calculations of landscape connectivity on habitat maps over time can better identify potential areas for species persistence and prioritize landscapes over large geographical areas (Early et al.

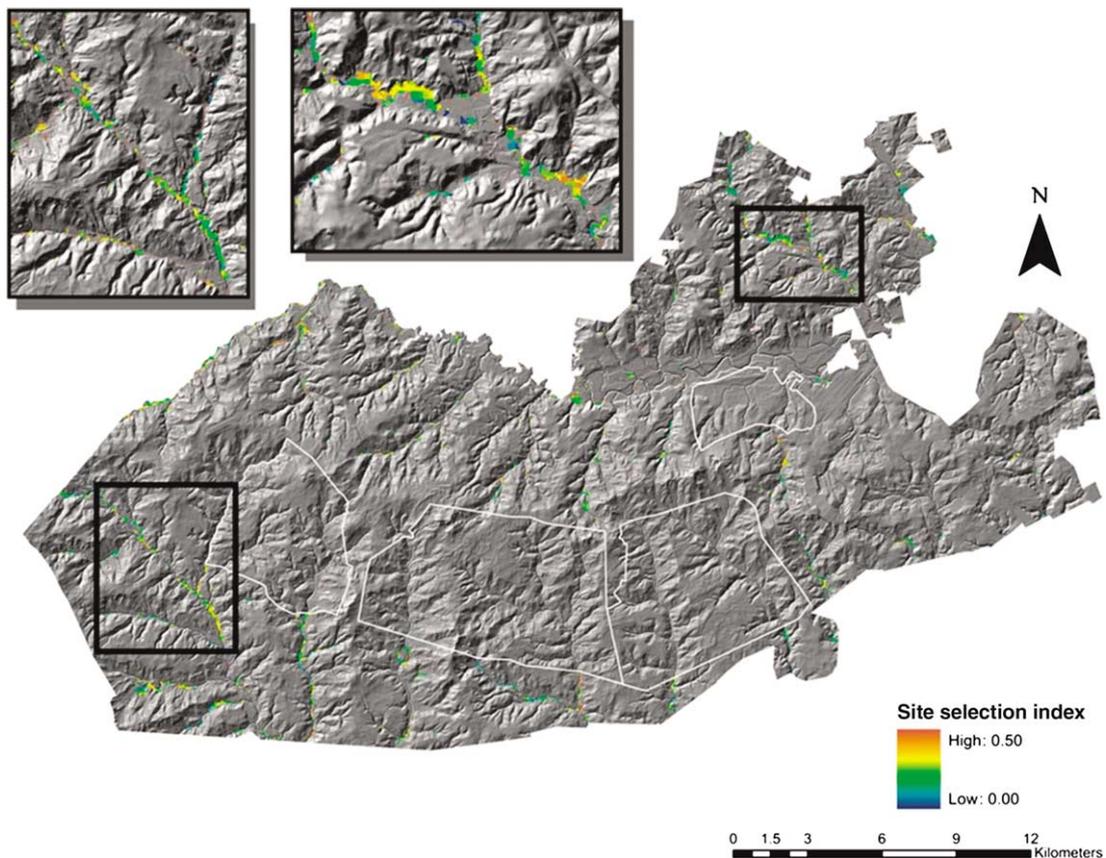


Figure 4. Priority areas for reintroduction efforts for *N. m. francisci* as predicted by Maxent model and our set-theoretic site selection index. Areas outlined in white represent the restricted military areas.

2008). Future modeling efforts should address changes in habitat connectivity over time to better understand the relationships between habitat dynamics and species persistence.

Conservation implications for the St. Francis' satyr

Predicted suitable *N. m. francisci* habitat is widely distributed across the study area, but most of this habitat is under-occupied by the species. The absence of *N. m. francisci* in locations identified as prime habitat may be explained by either methodological or ecological reasons. Methodologically, the absence may be a spurious effect of insensitivity of the environmental variables or habitat model to important latent variables such as host plant occurrence (Bartel 2008, Kuefler et al. 2008) – a long-recognized limitation of niche-based models (Green 1971). This includes mismatches of scale between the image data and the relevant environmental gradients. Ecologically, given the sedentary behavior of the species, the absence of *N. m. francisci* in prime habitat may also be driven by interactions of dispersal limitation and landscape dynamics.

Upland zones between stream drainages have low habitat value, and may thus impede butterfly dispersal to available habitat. Riparian corridors may serve as links between habitat patches within drainages (Kuefler and Haddad 2006), but rarely facilitate larger movements between drainages. These long-distance movements can occur between subpopulations, but have been observed only rarely (Kuefler et al. 2008). The spatial arrangement of habitat is also influenced by beavers, whose ecosystem engineering creates a shifting successional mosaic of habitat suitability and drives changes in butterfly occupancy (Bartel 2008).

A great contribution of predictive habitat maps to rare and endangered species management has been their ability to guide reintroduction and restoration efforts (Sexton et al. 2006). *Neonympha mitchellii francisci* subpopulations are currently located in three stream drainages outside military restricted areas. Subpopulations within a given stream drainage are separated by 700–1300 m and connected by contiguous riparian habitat, yet dispersal between subpopulations is infrequent (Kuefler et al. 2008). This metapopulation structure determines the placement of new subpopulations in reintroductions, suggesting two alternative reintroduction scenarios. To increase the viability of the metapopulation, reintroductions should be located either to: 1) accommodate more common smaller dispersal events, thus allowing genetic exchange, or 2) spread the risk of metapopulation extinction across a larger portion of stream network. Introducing individuals near established subpopulations may mitigate problems of small populations such as Allee effects and resulting low abundance levels (Stephens and Sutherland 1999), but spreading metapopulations across more watersheds may alleviate risk from concentrated habitat loss due to disturbance such as fire (or lack thereof, as we observe in this system with beaver impoundments). Since reintroduction efforts have not been previously attempted in this system, these two scenarios would pose competing hypotheses to evaluate successful establishment

and persistence and provide a rare experimental test of metapopulation theory at the landscape scale.

Conclusions

Applications of species distribution models to conserve rare species are numerous. We present a case study using *N. m. francisci*, a species restricted to a single location where urgent conservation is required to avoid extinction (Ricketts et al. 2005), yet this presence-only habitat modeling approach would apply broadly to many rare and endangered species in dynamic landscapes. Understanding spatiotemporal interactions between species persistence, habitat needs, and relationships with environmental factors is imperative for conservation planning of critically rare species. Defining habitat requirements and identifying environmental predictors of patch occupancy over time can improve recovery plans, offer adaptive management strategies to better inform conservation agencies for monitoring populations of rare and endangered species, and provide exact criteria for species status assignment.

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