ABSTRACT

BARTEL, REBECCA ANNE. Effects of Disturbance on Habitat Dynamics of a Rare Species. (Under the direction of Nick Haddad and Jim Gilliam.)

One of the most critical tasks in conservation planning for rare and endangered species is predicting how species respond to changing landscapes. Species abundance and distribution are impacted by spatial dynamics through habitat loss and fragmentation, and temporal dynamics of processes such as disturbance and succession. Knowledge of the potential distributions of critically rare or endangered species is necessary to assess species status and to guide species recovery plans. I examined responses of a rare species, the St. Francis' satyr butterfly, *Neonympha mitchellii francisci*, to changing environments using a combination of empirical studies, geospatial analyses, and mathematical modeling techniques.

First I used an observational study to evaluate how an ecosystem engineer, the beaver (*Castor canadensis*), influenced the presence and abundance of butterfly populations by affecting species richness and composition of wetland plant communities across local and landscape scales. Specifically, I assessed whether beaver engineering affected the persistence of larval host plants of *N. m. francisci* and impacted butterfly distribution in addition to overall biodiversity. Through field surveys of vegetation communities in habitat types across the successional gradient, I found that engineers create habitats where critical food plants persist for *N. m. francisci*. Engineers also increased plant species diversity by creating a combination of patch types across the landscape. This research shows how ecosystem engineers can play a role in both the conservation of a rare species, by influencing habitat availability and determining the composition of plant communities important for an endangered insect, and of overall plant species diversity by facilitating increased habitat heterogeneity.

To predict the spatial distribution of suitable environmental characteristics for a rare species, I created a habitat model based on remotely sensed geospatial data. Using a time series of calibrated Landsat Thematic Mapper satellite images, species occurrence data, and the Maximum Entropy modeling approach, I monitored spatio-temporal changes in habitat suitability for *N. m. francisci* to evaluate current habitat availability and to target sites for reintroduction efforts. Model results predicted suitable butterfly habitat is widely distributed across the study area, yet most suitable sites are unoccupied. 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 more exact criteria for species status assignment.

To further investigate effects of spatiotemporal changes in habitats on the distribution of rare species, I used a metapopulation approach. Metapopulation dynamics may depend crucially on habitat dynamics caused by disturbance and succession. While recent models have examined effects of disturbance on metapopulation size, my work is the first to evaluate impacts across different lengths of succession. To assess how landscape and species' characteristics affect metapopulation size, I used a spatially implicit patch transition model. I analyzed the effects of varying disturbance frequencies (low, moderate, and high) in different scenarios of successional length (fast, medium, slow) to cover the biological range of species' response. To assess how species sensitivity to habitat changes respond to shifting patch availability across the landscape, I compared three occupancy rules (early, late, or all habitats) and a range of colonization rates. I demonstrate that metapopulation size is influenced by a combination of factors including the speed of succession, disturbance

frequency, when patches are occupied (i.e., early or late successional stages), and colonization rate. Knowledge of successional speed and colonization rates can determine whether conservation strategies should concentrate on modifying landscape structure or habitat quality. Through evaluating how species respond to environmental changes across different models of disturbance and succession, we can make better conservation and management recommendations for rare species which utilize successional habitats.

Effects of Disturbance on Habitat Dynamics of a Rare Species

by
Rebecca Anne Bartel

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APPROVED BY:

Dr. Thomas R. Wentworth	Dr. Justin P. Wright
Dr. James F. Gilliam Co-chair of Advisory Committee	Dr. Nicholas M. Haddad Co-chair of Advisory Committee

DEDICATION

To Kristen Kostelnik, who is quite simply the best friend any person could ask for.

BIOGRAPHY

I was born in Livonia, Michigan in 1977 to Timothy and Carol Bartel. I have one younger brother, Adam. I spent my early years in Plymouth, Michigan and summered on Old Mission Peninsula. I believe the fond memories there in the woods and on the beach shaped my relationship with nature and interest in the outside world. My curiosity and independence were always encouraged. I completed a Bachelor of Science degree at Michigan State University where I majored in Zoology, concentrating in animal behavior and neurobiology. I then moved to Logan, Utah and pursued a Masters of Science degree in Wildlife Biology at Utah State University. Under the guidance of Dr. Fred Knowlton and encouragement of Dr. Mark Brunson, I began to envision my career path in academia and decided to continue my graduate education even further. Dr. Taylor Ricketts introduced me to Dr. Nick Haddad, who would become my Ph.D. advisor at North Carolina State University, at an Ecological Society of America meeting in 2002.

I moved to Raleigh, North Carolina in the summer of 2003 to become Dr. Haddad's second Ph.D. student at NC State in the department of Zoology. I have had the good fortune to work with a wonderful group of students, both undergraduate and graduate, and faculty members at NC State. The combined experiences of working on campus and at my field sites on Fort Bragg have shaped my thinking and approaches to both ecology and science in general. I am truly grateful to have had these opportunities.

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In my five years spent in the Department of Zoology at NC State, I've have the privilege to work with a broad range of people. So many of you have guided and supported me both professionally and personally, for which I will always be grateful.

First, I would like to thank my family for never questioning why anyone would want to do what I do. My mother, Carol Smith, has always encouraged and supported my pursuits. My brother, Adam Bartel, has constantly given me a practical viewpoint and his strength, both physically and figuratively has always been my foundation. My aunt and uncle, Sandy Schubach and Ed Zimney have both financially and intellectually supported all of my graduate work graciously. I would also like to thank Donna, Norm, and Kevin Lyttle for encouragement along the way.

This work has been financially supported through grants of the Endangered Species Branch of the U.S. Army through the Department of Defense. Erich Hoffman and Brian Ball have facilitated a creative research project and aided with logistical needs in the field. Their uncompromising support of this research and championing this cause to DoD is the main reason we were able to start this work at all, much less complete it. Jackie Britcher, Janet Gray, Pat Wefel, and Brian Hoogerwerf have also assisted with field issues and support.

My research would have not been possible without the support of my advisor, Nick Haddad. Nick has been a constant source of inspiration, ideas, and encouragement. Not only is Nick is an amazing ecologist, teacher, and mentor, but his never ceasing enthusiasm and positive outlook has continually motivated me. Nick's excitement has encouraged many of us to consider some difficult questions in ecology. He has a gift for challenging me to take

my research to the next level without ever making me feel inadequate or incapable. I can only hope one day I'll serve my students as well as he does.

In addition to Nick, my advisory committee has provided countless ideas and discussions that have resulted in improved research and techniques. Jim Gilliam, Tom Wentworth, and Justin Wright have all contributed to my investigations considerably. Rarely do I hear of anyone's entire committee having been to their field site or being "hands-on", and I am fortunate that is the type of committee I had during this experience.

There have been so many people at NC State that have contributed to my personal and professional development over the years. Rob Dunn, Kevin Gross, and George Hess have each helped me in troubleshooting research issues and discussing ideas in each addition to being wonderful friends. Thurman Grove served as my department head during most of my tenure and has given lots of insight into the administrative challenges of running our department with humor and wit. Wendy Moore, Susan Marschalk, Chris Smith, Kayde Brownlee, Dawn Newkirk, Dollie Moore, Meredith Henry, Dana Derosier, Marlu Bolton, and Dena Haughley have been an amazing administrative support team and have solved my problems over and over again both as a student and as President of ZGSA.

Living in the Triangle, I've had the benefit of interacting with people at all three of the major universities. Dean Urban, Pat Halpin, and Joe Sexton of the Landscape Ecology Laboratory at Duke University have considerably aided the development of my research related to spatial analyses in Ch. 2. Dean was one of the first people to suggest working with Nick for my Ph.d. program and was incredibly helpful in facilitating professional

relationships in the area. He continues to be a great mentor and soundboard for discussions and research development.

None of my field work would have been possible with the patience and perseverance of my field crews. Shannon Adcock, Sarah Andrews, Lauren Grove, and Liani Zabala were all enthusiastic and capable field technicians. Their witness to project development and challenging field conditions is greatly appreciated. They continued to remain upbeat regardless of vehicle problems, snakes, spiders, ticks, chiggers, and adverse weather. I can only hope I inspired them a tenth of what they've given me.

Over these past five years, I've watched our lab continue to expand and had the pleasure of working with a variety of people. Jessica Abbott, Megan Chesser, Ellen Damschen, Noa Davidai, Will Fields, Catherine Frock, Brian Hudgens, Brenda Johnson, Daniel Kuefler, Allison Leidner, John McAllister, Nicole Thurgate, Laura Vogel, Aimee Weldon, Johnny Wilson, and Dave Woodward have all been amazing labmates and colleagues. Ellen Damschen in particular was never-ending source of encouragement and strength and a constant cheerleader even from afar. She sets an amazing bar for productivity and mentorship. I'd also like to thank Will Fields specifically for being a constant source of both academic and personal entertainment and a fantastic officemate.

In addition to my labmates, I've meet many graduate students would have supported me through all the research and personal crises along the way. I could not have survived this without the friendship, encouragement, support, and comic relief of many of you. Nate Bacheler, Kayde Brownlee, Salinda Daley, Ellen Damschen, Christina Durham, Will Fields, Ari Friedlaender, Elliott and Lucie Hazen, Kristen Kostelnik, Erica Marsh, and Sunny Snider

made this experience possible and even fun (!). Seriously, their love and friendship made this process possible when I was ready to not continue. Kristen Kostelnik has been constant source of humor, insight, strength, inspiration, and integrity. Not only has she been an amazing ecologist and collaborator to me, but a travel partner, cat sitter, party planner, and my closest confidant. I can't imagine meeting this goal without her.

Lastly, I would like to thank my household, Brandon Puckett, Sam, Stella, and Lucy for their endless entertainment, companionship, friendship, and love. Brandon has been an amazing collaborator, MATLAB troubleshooter, backpacking and surf buddy, best friend, and partner to me. His easy-going nature is the calming force that has made my life infinitely happier. I am so grateful for his companionship and our team. Finally, special thanks to Sam, the four-legged love of my life, who has been by my side through 11 of 13 years of college. I can only imagine his version of all of this.

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CHAPTER 1: MAINTENANCE OF RARE SPECIES BY ECOSYSTEM ENGINEERS

A paper submitted to *Conservation Biology*

Rebecca A. Bartel, Nick M. Haddad, and Justin P. Wright

Abstract

Through physical alteration of their environments, ecosystem engineers can create and modify habitats, allowing more species to persist across the landscape. I evaluated how an ecosystem engineer, the beaver (*Castor canadensis*), influenced the presence and abundance of an endangered butterfly by affecting species richness and composition of wetland plant communities at local and landscape scales. I assessed whether beaver engineering influenced the persistence of larval host plants of St. Francis' satyr butterfly, *Neonympha mitchellii francisci,* and impacted butterfly distributions. I surveyed the vegetation communities in all stages of the wetland successional gradient, and I found that locally beavers create wetland habitats that support plant species not found elsewhere in riparian zones. Engineers also increased plant species diversity by creating a combination of patch types across the landscape. While my results confirm what others have found about engineering effects on plant diversity, I go further in showing a case where engineers also have a positive role in maintaining the distribution of rare animals. By creating unique plant communities, engineers enable establishment of plants that rare animal species depend on while also providing a diverse habitat structure. My research shows how ecosystem engineers can play a role in both the conservation of a rare species, by influencing habitat availability and

determining the composition of plant communities important for an endangered insect, and in the maintenance of overall plant species diversity by increasing habitat heterogeneity.

Introduction

By creating disturbances, ecosystem engineers have been shown to influence species diversity and community composition (Jones et al. 1997, Crooks 2002, Wright et al. 2002). Engineers can physically alter their environments and create habitats with unique communities relative to unmodified habitats (Jones et al. 1994, 1997) that can allow more species to persist across the landscape. Engineers can increase diversity in general (Lill and Marquis 2003, Wright et al. 2003, Badano and Cavieres 2006), but they may also be critical for maintenance of rare species (Pintor and Soluk 2006). Engineers can change the composition and diversity of plant communities (Wright et al. 2002, Anderson et al. 2006, Badano and Cavieres 2006) on which rare animal species rely for food, shelter, and other resources. Here, I examine how engineers can influence two conservation goals through creating habitat for a critically rare species and increasing biodiversity in general.

Rare species with smaller population sizes can be particularly sensitive to subtle changes in habitat dynamics (Harrison 1991, 1994). One pathway by which engineers can cause habitat changes is through modification of plant successional dynamics. Many populations of critically rare and endangered species respond to habitat requirements of specific successional stages (Menges 1990, Thomas 1994, Gutierrez and Harrison 1996, Walters et al. 2002, Thomas and Hanski 2004). Engineering can create conditions necessary for critical food resources (e.g., host plants), or provide the diverse habitat structure that

some animals may require (e.g., nesting trees) that may otherwise be unavailable with continued vegetative succession and no disturbance. While these species depend on disturbance to create new habitats for them to colonize (Pendergrass et al. 1999, Braun et al. 2001), disturbance can also increase extinction risk. Habitat modification can destroy standing vegetation including plant species that rare animals use as food or shelter. Engineering can cause patches to turn over quickly, creating a shifting mosaic of suitable and unsuitable habitat for many species across the landscape (Bormann and Likens 1979, Pickett and White 1985). The effects of engineering on species persistence can be determined by the proportion of modified habitats relative to unmodified habitats (Wright in review). I examined if engineering activities would maintain and create additional habitat patches for butterfly populations by creating a combination of different habitat types on the landscape.

The impacts of engineers on species diversity in general are dependent on the spatial and temporal scales of engineering (Wright and Jones 2006, Hastings et al. 2007). Ecosystem engineers have been shown to increase diversity at the landscape scale (Wright et al. 2003). To do so, engineers must create patches with unique conditions that support species to establish and persist in engineered habitats that are not present in unmodified patches (Jones et al. 1997, Wright et al. 2002). At the local scale, engineers may increase or decrease species diversity by changing habitat complexity (Crooks 2002, Pringle 2008) or by altering species colonization and establishment (van der Valk 1981).

Most studies of ecosystem engineers have focused on diversity as a response variable. My study primarily concerns the effects of engineers on one rare species. An open question is: do ecosystem engineers increase diversity generally and also increase habitat availability

for individual rare species? To a large extent, the effect of engineering on overall diversity is determined by the proportion of species in the regional species pool that specialize in each habitat type (Badano et al. 2006). However, rare animals may not depend on the entire species pool; instead, they may utilize specific plant species. Therefore, engineering can impact rare species by affecting the persistence of particular plant species that animals rely on without increasing overall plant species diversity. Through temporal effects on succession across the landscape (McMaster and McMaster 2000, Bruno et al. 2003), engineers can influence total species richness and plant community composition by creating a variety of patches at different successional stages (Wright et al. 2002, 2003). I test whether ecosystem engineers benefit both the populations of one rare species and overall plant diversity.

At my study site, beavers (*Castor canadensis*) are the primary agent of disturbance responsible for the creation and maintenance of wetland habitats (Kuefler et al. 2008). I evaluate how the engineering activities of beavers such as building dams, flooding existing vegetation, and initiating local vegetative succession affect plant species composition and diversity over time. One animal impacted by these modifications is the endangered St. Francis' satyr butterfly, *Neonympha mitchellii francisci*. The known population of *N. m. francisci* ranges between 700-1400 adult individuals, with their global distribution limited to approximately 30 ha in central North Carolina (Kuefler et al. 2008). The butterflies occur in several subpopulations in wetland meadows along streams, where their presumed larval host plants (*Carex* species) are found. While butterfly presence may depend on specific plants, the diversity of habitat structure and community composition may also strongly influence

butterfly dynamics by providing shelter and additional food resources. Wetlands may also be important sources of plant diversity in this landscape. I examine how engineers affect plant diversity in a system with important consequences for rare species and compare my results to previous work that has focused more narrowly on the effects of engineering on plant communities.

Methods

Study Area

I conducted my research on Fort Bragg military reservation in south central North Carolina (latitude 35°07′30″N, longitude 79°08′30″ W) located within the sandhills region of the Inner Coastal Plain physiographic province (Figure 1.1). Locations of study sites are confidential due to the possible risk of butterfly collecting. The predominant vegetation consists of longleaf pine (*Pinus palustris*) communities that vary along a moisture gradient from xeric entisols to mesic/wet ultisols (Gray 1999). Mean annual temperature is 16.3 º C and mean annual precipitation for 1950-2004 is 1,178.8 mm/yr. Elevations range from 120–220 m.

Field surveys

To assess beaver effects on butterfly host species and plant diversity from plot to landscape scales, I studied all stages of the wetland successional gradient. I selected sites based on visual analysis of the study area using digital aerial photographs available from 1996-2005 (flown at 2-year intervals) in addition to an existing beaver impoundment vector

layer from 2000 that was updated in 2005 through ground surveys (Alan Schultz, *personal communication*). There were > 120 total beaver sites identified in total. I selected sites from four stream drainages based on the availability of various states of beaver activity. Because the borders, sizes, and shapes of beaver sites are dynamic, we used global positioning system (GPS) hardware (Trimble® GeoXM™ Pocket PC) to document all spatial changes in previously known beaver impoundment areas and to record new areas of beaver activity. Through ground surveys, I classified sites by location, size, and beaver presence/absence, and then categorized by wetland type: occupied by beavers (open water), recently abandoned by beavers (early successional vegetation), degraded beaver sites (late successional shrubby or woody vegetation), or unmodified areas with no evidence of beaver activity. *Open water* sites may or may not have active beaver colonies, but often still have standing water due to an impoundment. Vegetation in open water sites is limited primarily due to standing water and is generally adjacent to the upland. Overall canopy cover is < 15%. *Early successional* sites are typically dominated by herbaceous plants, and have little to no standing water and high light penetration (< 50% canopy cover). *Late successional* sites are characterized by shrubs and/or trees, no standing water, and lower light penetration (>50% canopy cover). *Unmodified* areas are stream stretches > 200 meters where beaver signs such as dams, chewed trees, or cut vegetation were absent. Percentages of canopy cover in unmodified sites vary, but are typically > 50%. Three replicates of each patch type were assessed on each of four stream drainages (C, D, E, and I) for a total of 48 patches. Here I define a patch as a single area of one habitat type. Subpopulations of *N. m. francisci* occur on stream drainages

D and E; while a single remnant subpopulation exists on C, which may have been one individual disperser. Butterflies have never been observed on stream drainage I.

In summer 2005, I surveyed vegetation using 1-m^2 quadrats (N = 614, range = 144-164 plots/drainage) to determine plant community diversity and composition. Because open water patches tended to be larger in area, I surveyed a maximum of 30 plots adjacent to the pond edge with equal distance between plots (N = 212 total open water plots). In all other habitat types, I located plots along transects 1 m from the stream edge or standing water with 10 m between consecutive plots (range = 124-143 total plots in each habitat type). I delineated the borders of all sites using topographic breakpoints where the wetland met the upland interface. I identified all plants in each plot to species when possible, and assigned a percent cover value, with values of individual species ranging from 0-100% and summed cover values for a plot greater than 100% possible when multiple strata were present (Peet et al. 1998).

I used sample-based rarefaction methods to calculate species accumulation curves for the 2005 data using EstimateS 7.5 (Colwell 2005) to evaluate whether my samples were effectively capturing most of the species in each patch. To ensure adequate sampling of the plant communities, I expanded plot sizes in a subset of the original plots to 3x8 m in 2006 (N = 219). I used the location of the 1x1 m plots from 2005 to guide placement of the larger plots, using the smaller plot as one of the corners nested in the larger plot. Each wetland patch contained between 3-6 larger plots based on area measurements of total patch. In addition to the larger plots, I resampled the smaller 1x1 m plots (N = 219) that occurred within the larger plots for all wetland patches. For most analyses, I used data from the larger

3x8 plots from 2006. To evaluate influences of likely host plant species on butterfly population sizes, I used data collected from 1x1 m plots because I had consecutive data for plots from 2005 and 2006, which coincided with estimates of butterfly populations.

Plant species identification

All plants were identified using the nomenclature of Radford et al. (1964). In some cases I used updated nomenclature from Weakley (2005) and the United States Department of Agriculture Natural Resources Conservation Service Plants Database (USDA NRC 2008) (http://plants.usda.gov/). I indentified all plant species to growth (e.g., shrub), life cycle (e.g., perennial) and to genus and species when possible. All unknown species were identified from samples or photographs taken in the field, compared with specimens at the North Carolina State University Herbarium, and verified with regional botanical experts. When I was unable to identify plant species to genus (less than 3% of all species), I removed them from all datasets prior to analyses.

Data analysis

I first assessed how composition of host plants influenced butterfly patch occupancy and habitat distribution. Subpopulation estimates for *N. m. francisci* were calculated by using both modified Pollard-Yates transect counts (Pollard 1977) and mark-release-recapture techniques (see Kuefler et al. 2008 for details). Next, I examined how ecosystem engineers affected plant abundance and composition in butterfly habitats. Finally, I tested for effects of engineering more generally on total plant diversity and composition across spatial scales.

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. I focused my analysis on the percent cover of six species of *Carex*: *C. atlantica, C. glaucescens, C. lonchocarpa, C. lurida, C. mitchelliana,* and *C. stricta.* I also grouped several less observed species that occupied on average less than 0.05 percent cover in all habitat types in an 'other' category (*C. collinsii, C. debilis, C. muehlenbergii,* and *C. turgescens*). To meet assumptions for a normal distribution of variance, I used an arcsine transformation on percentage cover estimates. I also evaluated correlations of averages of percent cover between individual *Carex* species by comparing Pearson correlation coefficients for 2005-2006 1x1 m plots. To examine the effects of host plant percent cover and butterfly demographics, I used linear regressions of percent cover estimates of individual *Carex* species and existing population estimates of *N. m. francisci* from 2005-2006 (Kuefler et al. 2008). Because a single estimate of butterfly populations may include several patches, I aggregated estimates of percent cover of *Carex* species to match the spatial scale at which butterfly population estimates were previously assessed (see Kuefler et al. 2008 for details). To quantify the characteristics of the host plant community which determine butterfly presence, I compared estimates of *Carex* percentage cover, total percentage cover of all observed plant species, and total species diversity for all patches using a Classification and Regression Tree (CART) model (Breiman et al. 1984). Using the *tree* package in the R statistical computing language (Ripley 2007, R Development Core Team 2007), I fit a CART using butterfly presence and absence data to model the probability of butterfly presence

based on percent cover of various *Carex* species. CART models have several features that are useful for predicting patterns in complex ecological data (De'ath and Fabricius 2000, Vayssiéres et al. 2000). CART models: (1) are nonparametric and therefore do not assume any particular distribution, (2) accommodate contingencies and multi-modal distributions, (3) allow for the combination of both categorical and numeric predictor variables, and (4) provide easy visual interpretation of explanatory variables (De'ath and Fabricius 2000). I evaluated both the overall misclassification rate and a confusion matrix of butterfly presence and absence.

To examine how differences in composition and percentage cover of host plants influenced butterfly patch occupancy and habitat distribution, I used several nonparametric techniques. First, I performed an indicator species analysis using estimates of percent cover for the seven *Carex* taxa (*C. atlantica, C. glaucescens, C. lonchocarpa, C. lurida, C. mitchelliana, C. stricta,* and the 'other' Carex group which included four species: *C. collinsii, C. debilis, C. muehlenbergii,* and *C. turgescens)* to test whether certain species were present in *N. m. francisci* habitats (McCune and Mefford 2005). I used the indicator value (fidelity of occurrence and relative abundance) of species in clusters or types (Dufrene and Legendre 1997). Following 5000 randomizations, I used a Monte Carlo test of significance to test statistical differences between indicator values. To test for differences between *Carex* composition and percent cover in *N. m. francisci* habitats vs. unoccupied sites, I used a Multi-Response Permutation Procedure (MRPP; Mielke and Berry 2001). I specified a Sorenson distance measure and defined *N. m. francisci* habitats as patches at which I have documented butterfly occurrences (McCune and Grace 2002, McCune and Mefford 2005).

To assess the effects of engineering on plant communities that support *N. m. francisci*, I first examined how beaver activities affected different species of *Carex*, the proposed host plants of *N. m. francisci*, at the patch scale. I performed a second indicator species analysis using percent cover estimates of the seven *Carex* taxa as previously described to test whether certain species were more associated with a single habitat type than others (McCune and Mefford 2005). I then used a MRPP (Mielke and Berry 2001) to test for differences between *Carex* composition and percent cover in all habitats among the different habitat types (McCune and Grace 2002). Additionally, I evaluated differences between *Carex* abundance on stream drainages with and without known *N. m. francisci* subpopulations among the different habitat types using general linear models (GLM, SAS Institute Inc. 2004).

To evaluate how engineering affected local plant species diversity, I calculated total species richness for each 3x8 m plot and each patch and then averaged results for each habitat type. I then calculated percent cover for each plot by summing percent cover of each individual species and for each patch by averaging total percent cover across all plots. I tested for differences in species richness between habitat types using GLMs, while mixed models with habitat type and drainage as fixed and random effects, respectively, were used to test for differences in total percent cover (SAS Institute Inc. 2004).

To test whether beavers increase plant species diversity across spatial scales to that found in previous engineering studies with plants, I compared species richness estimates in the four habitat types at three different scales: plot-level (range = 3-6 plots/patch), patch-level (N = 48), and landscape-level (N = 4 habitat types). Alpha diversity (diversity among

samples, Whittaker 1960) within plots was calculated as the average species richness across plots (N = 219). I used a richness estimator, Chao 2 (Chao 1987), a non-parametric method for estimating species richness from samples containing both common and rare species (Colwell and Coddington 1994) for all other scales. I compared diversity at the patch scale by calculating Chao 2 estimates for each site (N = 48 patches), and then at the landscape-level by calculating Chao 2 values for all patches by habitat type based on incidence of species across patches (N = 4 habitat types; Colwell 2005). Differences in total percent cover and species diversity and in differences in variation in species diversity between drainages and habitat types were examined similarly to methods used at the plot scale using GLMs and mixed models.

To estimate the importance of beaver-modified patches for maintenance of species richness at the landscape scale, I used my plant community data to run Monte Carlo simulations of landscapes containing different proportions of beaver-modified habitats. For all simulations, plots from different patches within the same habitat type were pooled. I randomly selected plots from different habitat types to generate simulated landscapes of 48 total patches (the number of plots sampled in the least-intensively sampled habitat) with proportions of plots from unmodified habitat ranging from 0% to 100% forest in ten percentile increments. Based on analysis of 2005 aerial photographs, 58% of modified habitat is in the open stage, 25% in the early stage, and 17% in the late stage. After randomly selecting the appropriate number of patches from the pool of forested patches, the remaining patches in the simulated landscapes were randomly selected from the three modified habitats (open, early, and late) in proportions that reflect the current relative distribution of the three

modified habitat types. For example, to simulate a landscape containing 50% beaver-modified and 50% forested riparian zone, I randomly selected 24 plots collected in forested riparian zones, 14 plots from open habitats, 6 plots from early habitats, and 4 plots from late habitats. I replicated this process 100 times at each level of patch cover and calculated the Chao 2 species richness estimator for each simulated landscape to estimate the total number of species present in the landscape.

Results

From 2005-2006 I observed approximately 181 different species of plants, with 139 identified with certainty (see Appendix A for complete species list). Unidentified species (N = 42) were assigned to genus when known (e.g., unknown *Vaccinium*) or growth form (i.e., unknown shrub) or otherwise removed prior to analyses. Most of these species are perennial (> 90%). The majority of the plants were herbs (104 species). Among these I found 39 graminoids (including 10 species of *Carex*). I also identified 17 taxa of shrubs, 25 tree species, and 15 taxa that could be classified as either shrub or tree species. The remaining taxa were ferns and vines (4 and 7 species respectively).

In 2005 and 2006, analyses of percent cover estimates of *Carex* showed statistically significant relationships between *C. atlantica* and *C. mitchelliana* (rho = 0.471, P = 0.001; rho = 0.520, P < 0.001 for 2005 and 2006 respectively; Table 1.1). In 2005, there was also a positive correlation between *C. atlantica* and *C. lurida* (rho = 0.714, P < 0.001), as well as the 'other' *Carex* group (rho = 0.577, P < 0.001). *C. lurida* was also significantly correlated with the 'other' *Carex* group in 2005 (rho = 0.757, P < 0.001), and with *C. lonchocarpa* in

2006 (rho = 0.484, P < 0.001). Percent cover of *C. mitchelliana* was significantly positively related to butterfly population sizes in 2005-2006 (P = 0.002, r^2 = 0.82, Figure 1.2).

CART models showed that estimates of percent cover of > 0.6% *C. mitchelliana* predicted butterfly presence most effectively. The tree had a residual mean deviance of 0.497. The model correctly classified six of eight presences (sensitivity = 0.75) and 37 of 40 absences (specificity = 0.925), for a total classification accuracy of 89.6%. On stream drainages with known butterfly subpopulations, I observed five patches occupied by *N. m. francisci* containing abundances of > 0.6% of *C. mitchelliana* consisting of engineered early and late successional habitats (Figure 1.3a). Two additional patches occupied by butterflies had no observed *C. mitchelliana*. Of the four patches with *C. mitchelliana* percent cover of > 0.6% in stream drainages without butterfly subpopulations, one *N. m. francisci* was observed once in 2003 in one early successional patch (Figure 1.3b). The remaining patches with higher densities of *C. mitchelliana* were late successional and unmodified habitats (Figure 1.3b).

Using indicator species analysis, I found that *C. atlantica* and *C. mitchelliana* were statistically significant indicators for *N. m. francisci* habitats (P = 0.002 for each species). The average relative abundance of *C. atlantica* and *C. mitchelliana* in *N. m. francisci* habitats was 88% for each species. The average relative frequency in butterfly habitats for *C. mitchelliana* (52%) was higher than the relative frequency of *C. atlantica* (37%). The indicator values which combine the relative abundance and relative frequencies of each species in each habitat type were 55.0 and 66.2 respectively for *C. atlantica* and *C. mitchelliana* in *N. m. francisci* habitats (Table 1.2). MRPP also supported *N. m. francisci*

habitats as compositionally different in *Carex* communities than habitats which did not support butterfly populations. The chance-corrected within-group agreement statistic, A, was 0.03 (P = 0.005), where A = 1 when all items are identical within each group (Mielke and Berry 2001).

Indicator species analysis also showed differences in *Carex* community composition between different patch types (Table 1.3). *C. atlantica* was significantly more frequently observed in late successional habitats (P = 0.007), while *C. mitchelliana* was significantly more frequently observed in early successional habitats than other habitat types (P = 0.007). *C. lonchocarpa* was the only *Carex* species found more frequently significantly in unmodified habitats (P = 0.067; Table 1.3). MRPP also confirmed differences in *Carex* abundance and presence between habitat types (A = 0.035, P = 0.022).

I detected significant differences in percent cover between stream drainages for *C. mitchelliana* ($F = 5.89_{15, 47}$, P = 0.003) and *C. glaucescens* ($F = 5.98_{15, 47}$, P = 0.002). I found no significant differences in *Carex* percent cover between patch types, or interactions between stream drainage and patch type. While most of the estimates of percent cover *Carex* species were highest in at least one type of the engineered habitats, several species were also never observed in at least one patch type (Figure 1.4).

Plant species richness at the plot scale was the highest in unmodified habitats ($\overline{X}$ = 25) and increased slightly with successional stage (range = 14-20, Figure 1.5). Mixed models showed statistically significant differences in species richness among both habitat types at the plot scale ($F = 23.35_{3, 214}$, P < 0.001) and drainages ($F = 2.79_{3, 214}$, P = 0.04). The only significant difference among stream drainages at the plot scale was between stream

drainages C and I, where butterfly subpopulations currently do not occur. Open water and unmodified habitats were significantly different from all other habitat types. While early and late successional habitats were both significantly different from open water and unmodified patches, they were not significantly different from one another (Figure 1.5a). With further analysis, I determined that these differences at the plot scale were explained by differences in total percent cover ($R^2 = 0.36$, $F = 123.86_{1, 219}$, $P < 0.001$). At the patch scale, I found statistically significant differences in species richness between patch types but not among drainages in estimated species diversity ($F = 4.28_{3, 41}$, $P = 0.01$), with the biggest difference in species diversity between open water and early successional habitats (Figure 1.5b). I did not observe significant differences in patch scale diversity between the stream drainages ($F = 2.05_{3, 41}$, $P = 0.122$).

Monte Carlo simulations showed estimated species richness was higher in beaver engineered than in unmodified habitats (Figure 1.6). The results of randomly sampling from all four habitat types on the landscape did not differ from those of sampling solely from engineered habitats (Figure 1.6). This is supported by my observations of species turnover; while most of the plant species found in unmodified habitats (N = 124) were also present in engineered habitats, 57 of the species in engineered habitats were not found in unmodified habitats (31% of total species observed). I found the maximum species richness occurred with a 70:30 ratio of engineered and unmodified habitats on the landscape (Figure 1.7). This caused beaver engineering to increase landscape-level species diversity by 15% over a landscape with no patches modified by beaver.

Discussion

I demonstrate that engineers have important roles in both creating habitat for a critically rare species and increasing biodiversity in general. While my results confirm what others have found about engineering effects on plant diversity, I go further in showing a case where engineers also can have a positive role in maintaining the distribution of rare animals. By resetting vegetative succession, engineers facilitate conditions needed by critical food plants that serve as resources for animals. Locally, beavers create wetland habitats that support plant species not found elsewhere in riparian zones. Engineers also increase plant species diversity by creating a combination of patch types across the landscape.

Beavers as ecosystem engineers can potentially have strong effects on abundance and species distribution of rare animals by influencing the community dynamics of plant species that they depend on. These effects are scale-dependent. The presence and abundance of *N. m. francisci* are strongly correlated to the occurrence and abundance of their presumed host plants, *C. mitchelliana*, at a local scale. I observed significant differences in composition and abundance in *Carex* communities in engineered patch types. *C. mitchelliana* was significantly more frequent and abundant in engineered early successional sites. At the landscape scale, engineering can influence the distribution of butterfly habitats by continuously producing new habitat patches. Determining this ratio for butterfly habitats requires additional analysis of butterfly spatial population dynamics.

The effects of beaver engineering on butterfly distributions depend on how beavers impact the presence and abundance of their presumed host plant. Although caterpillars have never been observed feeding in the wild despite searches over the last 20 years, previous

feeding experiments and field surveys (Kuefler et al. 2008) suggest that the primary larval host plant of *N. m. francisci* is *C. mitchelliana* in addition to other *Carex* species. I cannot rule out that *C. mitchelliana* is strongly correlated with the presence of another plant species that is the true host plant of *N. m. francisci*. But my results support that *C. mitchelliana* strongly influences the presence and abundance of butterflies. Indicator analysis suggested that *C. mitchelliana* best predicted the presence of butterfly habitat. CART models also showed abundance of *C. mitchelliana* was the strongest indicator of *N. m. francisci* presence. Yet it also misclassified several occupied sites containing no *C. mitchelliana*, indicating there may be additional factors such as possible alterative host plant or butterfly dispersal limitation affecting butterfly distributions of *N. m. francisci*.

Additionally, I observed two sites with high abundances of *C. mitchelliana* in unmodified habitats on creeks without known *N. m. francisci* subpopulations. This may be the result of potential limitations in site selection. The unmodified habitat with the highest amount of *C. mitchelliana* is immediately adjacent to an engineered early successional habitat with a known remnant population of *N. m. francisci*. Although I utilized consistent criteria in my site classification to delineate habitat types, the proximity of these sites may demonstrate the shared effects of nearby engineering or other types of disturbance. The other unmodified site with high density of *C. mitchelliana* is interesting in that butterflies have never been observed on this stream drainage and *C. mitchelliana* is only present in two of the 12 sites on the creek. These exceptions provide support for assessment of total plant diversity in order to understand butterfly population dynamics. Butterfly populations may require the diverse habitat structure in addition to host plants (Hall et al. 2001).

My work also demonstrates that engineering can impact dynamics of a rare species population through determining the patch transition rates and spatial distribution of their required habitats. The entire butterfly population is comprised of a metapopulation structure of multiple subpopulations of *N. m. francisci* within a watershed (Kuefler et al. 2008). Local extinctions of individual subpopulations will increase the likelihood of metapopulation extinction. Metapopulation theory assumes that populations persist through colonization and extinction of subpopulations, yet changes in environmental suitability or habitat structure may affect these dynamics and ultimately influence metapopulation persistence (Hanski and Gaggiotti 2004). The distribution and viability of *N. m. francisci* subpopulations depend on ecosystem engineering to regenerate wetlands habitat to earlier successional stages. With continued vegetative succession and no disturbance, local extinctions of butterfly populations are likely to occur (Kuefler et al. 2008). Yet, beaver engineering can also flood occupied habitats and kill host plants (and larval forms of *N. m. francisci*). Disturbances in these sites can impact butterfly habitats quickly, resulting in a shifting successional mosaic of habitat patches across the landscape. Engineering can accelerate these changes—in a single year between 2005 and 2006, I observed six of 12 early successional patches were recolonized by beavers and flooded. This reduced the abundance of *Carex* and decreased overall plant species richness. Natural disturbances such as hurricanes or wildfires can also affect overall plant species diversity and turnover and plant availability for animal species. Understanding the optimal amount of engineering needed is essential to predict patch occupancy patterns of *N. m. francisci*. Habitat tracking metapopulation models can evaluate the interactions among

disturbance frequency, successional rate, patch occupancy and rates on metapopulation persistence (Ch. 2).

In addition to impacting the persistence of a rare animal, engineering also affected local plant community composition and abundance, with the highest levels of total plant species diversity in open water habitats. At the landscape scale, by increasing habitat heterogeneity, beavers as engineers can create wetland habitats capable of supporting herbaceous plant species not found elsewhere in the riparian zone (Wright et al. 2002). Similarly, I found that the high levels of plant species diversity requires a mixture of unmodified habitats and engineered habitats at different successional stages. Landscape simulations suggested optimal levels of engineering for plant diversity at approximately 70% of the total habitats.

My study also places the strong role that beaver play as ecosystem engineers in maintaining regional diversity and the population and spatial dynamics of rare species in a global context (Table 1.4). Several studies have evaluated beaver dynamics in different environments including temperate forests in New York (Wright et al. 2002, 2003) and sub-Antarctic forests of Tierra del Fuego, Argentina (Martinez Pastur et al. 2006) and Cape Horn, Chile (Anderson et al. 2006). My results are consistent with others from North America showing that beavers increase diversity. Whereas my study demonstrates engineering impacts on native rare species, beavers are an invasive exotic species in South America (Anderson et al. 2006). Fourteen percent (9 of 63 species) of plant species found in engineered patches in Cape Horn were exotic (Anderson et al. 2006), while very few invasives were found in the North American sites (1 species in each site; Table 1.4).

Beaver-modified sites in Tierra del Fuego have higher levels of organic and inorganic nitrogen, which may allow some plant species to take advantage of the conditions in the engineered habitats (Lizarralde et al. 2004), further enabling establishment of other invasive species (Crooks 2002). Native *Nothofagus* forests in these areas cannot recover from long-term beaver engineering due to slow regeneration (Martinez Pastur et al. 2006), resulting in the creation of a more homogeneous plant community at the landscape scale (Anderson et al. 2006).

Because engineers can alter physical conditions of their environment, they are likely to impact overall species diversity. I provide evidence of a system where engineers also affect the persistence of a rare animal species through creating favorable conditions for the plants they depend on. Yet, it is unclear if broad patterns exist for combined effects on both rare species and biodiversity by different engineers. Engineering may also lead to trade-offs between the preservation of a rare species and conservation of species diversity in general. Engineers can positively affect the persistence of rare species without increasing total biodiversity across the landscape. Two conditions must be met to increase species diversity at the landscape scale. Engineers must create patches with a combination of conditions not present elsewhere in the landscape, and there must be species that can persist in engineered habitats that are not present in unmodified patches (Jones et al. 1997, Wright et al. 2002). In contrast, engineers can increase total species diversity, but rare species can be negatively affected by increased habitat heterogeneity if they depend on the environmental conditions of unmodified patches. Although I detected 57 plant species only present in engineered patches, I also observed 15 species (8% of total species) occurring in only unmodified

habitats. Just as with *N. m. francisci*, a rare plant, the sandhills fire lily (*Lilium pyrophilum*), occurs in engineered sites. Beavers as ecosystem engineers have a short term negative effect on the lily. Three of 22 total lily populations on Ft. Bragg have been recently eliminated due to beaver impoundment (K. Kostelnik, *pers. communication*). It remains to be seen how well this plant recovers after beaver disturbance.

Beavers are one of the most familiar examples of ecosystem engineers because of the magnitude and legacy effects of their impacts on the environment, but the implications of my results are likely to extend to other engineers. Engineers can perform many roles and functions; some engineers are endangered (Bangert and Slobodchikoff 2006, Buse et al. 2008), while others are considered exotic or invasive (Crooks 2002, Castilla et al. 2004, Anderson et al. 2006). Engineering can facilitate further species invasion (Anderson et al. 2006, Badano et al. 2007) or aid the persistence of rare species (Pintor and Soluk 2006). My work is unique in assessing these combined impacts in a system where disturbance is necessary for maintenance of an endangered species and also conserves total biodiversity. Many animal species have become threatened or endangered as the result of modifications of disturbance dynamics (Pendergrass et al. 1999, Kaye et al. 2001). If ecosystem engineers are the main agents of patch dynamics in areas with altered disturbance regimes, then the conservation and management of these engineers will be vital to conserve habitat for any affected imperiled species and to manage against the spread of invasive species. Understanding the role of engineers in ecosystems can focus conservation, habitat management, and restoration efforts in ecosystems with critically rare species.

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Table 1.1. Pearson correlation coefficients for *Carex* species at the patch scale 2005-2006. Estimates of percent cover were arcsine transformed to meet assumptions for a normal distribution of variance.

Species	Pearson correlation coefficients for 2005 plots (N = 583)						
	Carex atlantica	*Carex glaucescens*	*Carex lonchocarpa*	*Carex lurida*	*Carex mitchelliana*	*Carex stricta*	Other *Carex*
Carex atlantica		-0.150	-0.106	0.714*	0.471*	-0.053	0.577*
Carex glaucescens	-0.103		-0.188	-0.034	-0.182	-0.081	-0.129
Carex lonchocarpa	-0.122	-0.059		-0.800	-0.127	0.053	-0.108
Carex lurida	-0.060	-0.005	0.484*		-0.076	-0.032	0.757*
Carex mitchelliana	0.520*	-0.107	-0.125	-0.038		0.111	0.032
Carex stricta	NA	NA	NA	NA	NA		-0.075
Other *Carex*	-0.042	-0.110	0.063	-0.080	-0.202	NA	
Carex mitchelliana *Carex lonchocarpa*	Pearson correlation coefficients for 2006 plots (N = 221)						

* = $P \leq 0.05$

Table 1.2. Indicator values comparing relative frequency and abundance of *Carex* species in sites occupied/unoccupied by *N. m. francisci* populations. Calculated with methods of Dufrene and Legendre 1997.

		Monte Carlo Test of Significance	
Species	Group*	Average	P-value
Carex atlantica	2	55.0	0.002
Carex glaucescens	1	41.7	0.240
Carex lonchocarpa	2	14.3	0.760
Carex lurida	2	11.2	0.759
Carex mitchelliana	2	66.2	0.002
Carex stricta	1	2.4	1.000
Other *Carex*	2	24.9	0.659

* where 1 = *N. m. francisci* absent, 2 = *N. m. francisci* present

Table 1.3. Indicator values comparing relative frequency and abundance of *Carex* species among patch types. Calculated with methods of Dufrene and Legendre 1997.

		Monte Carlo Test of Significance	
Species	Group*	Average	P-value
Carex atlantica	3	25.9	0.071
Carex mitchelliana	2	29.4	0.071
Carex glaucescens	1	33.2	0.284
Carex lonchocarpa	4	27.2	0.066
Carex lurida	4	14.3	0.423
Carex stricta	2	7.7	1.000
Other *Carex*	3	12.5	0.957

* where 1 = open water, 2 = early successional, 3 = late successional, and 4 = unmodified habitats

Table 1.4. Comparison of several studies observing the impacts of beavers as ecosystem engineers on plant communities.

Variables	*Wright et al. 2002, 2003*	*Anderson et al. 2006* *Martinez Pastur et al. 2006*	*Bartel et al. 2008*
Location	New York, USA	Cape Horn, Chile Tierra del Fuego, Argentina	North Carolina, USA
Latitude, Longitude	44°00'N, 74°13'W	55°59'S, 67°16'W	35°07′N, 79°08′W
Elevation range (m)	657–823	0–150	120–220
Mean annual temperature (°C)	4.4	4.8	16.3
Mean annual precipitation (mm)	1010	500–650	1180
Predominant vegetation type	*Alnus* forest	*Nothofagus* forest	*Pinus* forest
Relative succession rates	Slow	Moderate	Fast
Plot size(s)	0.5 x 1.0 m^2	0.5 m^2	1.0 m^2, 3.0 x 8.0 m^2
Beaver history	Native, reintroduced ~ 1910	Exotic, introduced in 1946	Native, reintroduced in 1939
Beaver densities (colonies/km)	0.5–0.7	0.2–5.8	Unknown
Beaver average occupancy rates, (range)	4.8 years (1–20)	(5–15)	Unknown
Total # of species (herbaceous layer)	125	67	158
Estimated landscape species richness	59-67 (in both habitats)	28-63 (in both habitats)	148-168 (in all habitats)
Species similarity between engineered/ not engineered (Mean Morista-Horn value, p-value from ANOVA)	<0.1, $p < 0.001$	~0.35, $p = 0.14$	0.21, $p = 0.0012$
Increased local species richness?	No	Yes	No
Increased landscape species richness?	Yes	No	Yes

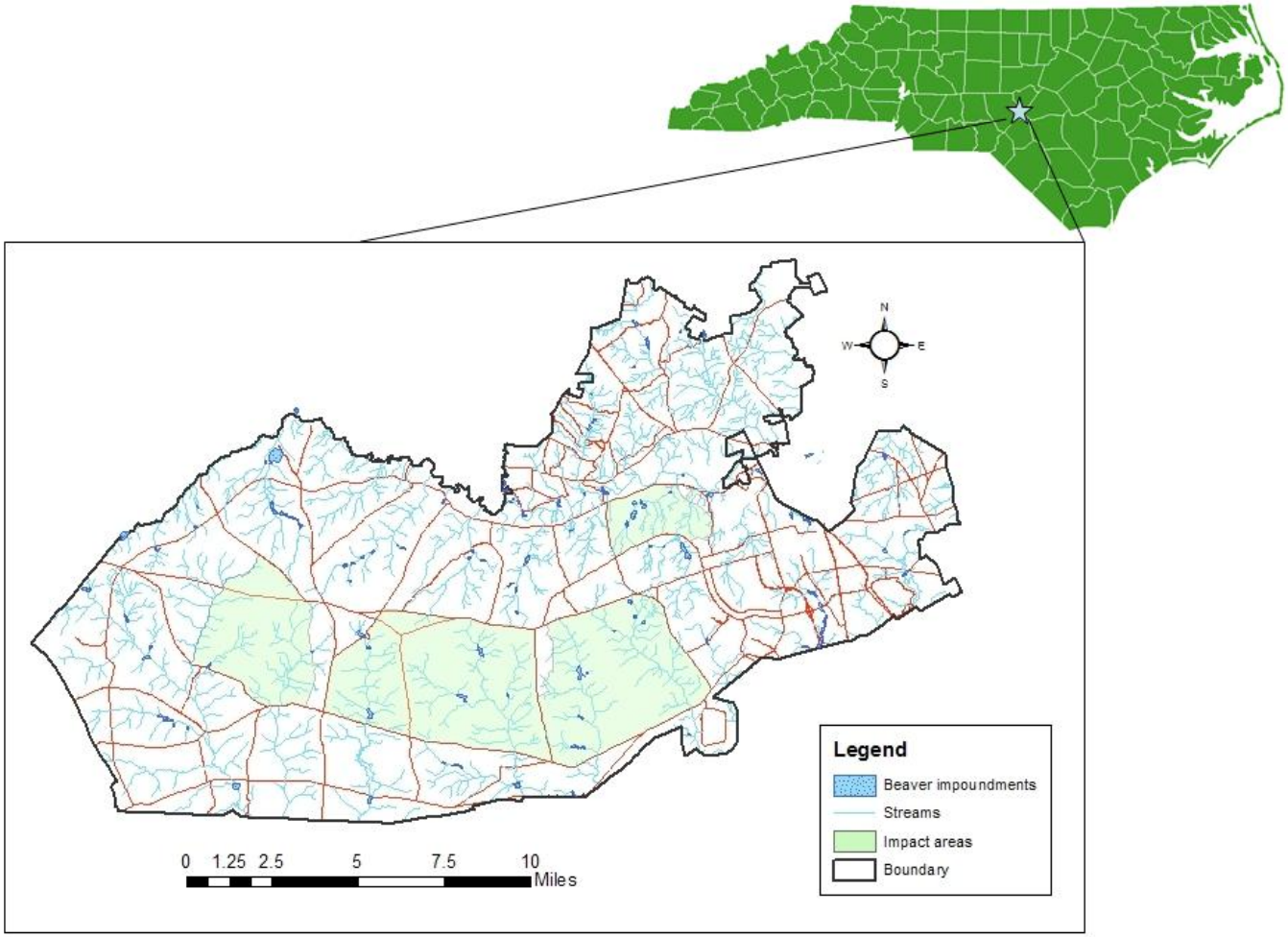

Figure 1.1. Map of all beaver impoundments in study area on Ft. Bragg, North Carolina.

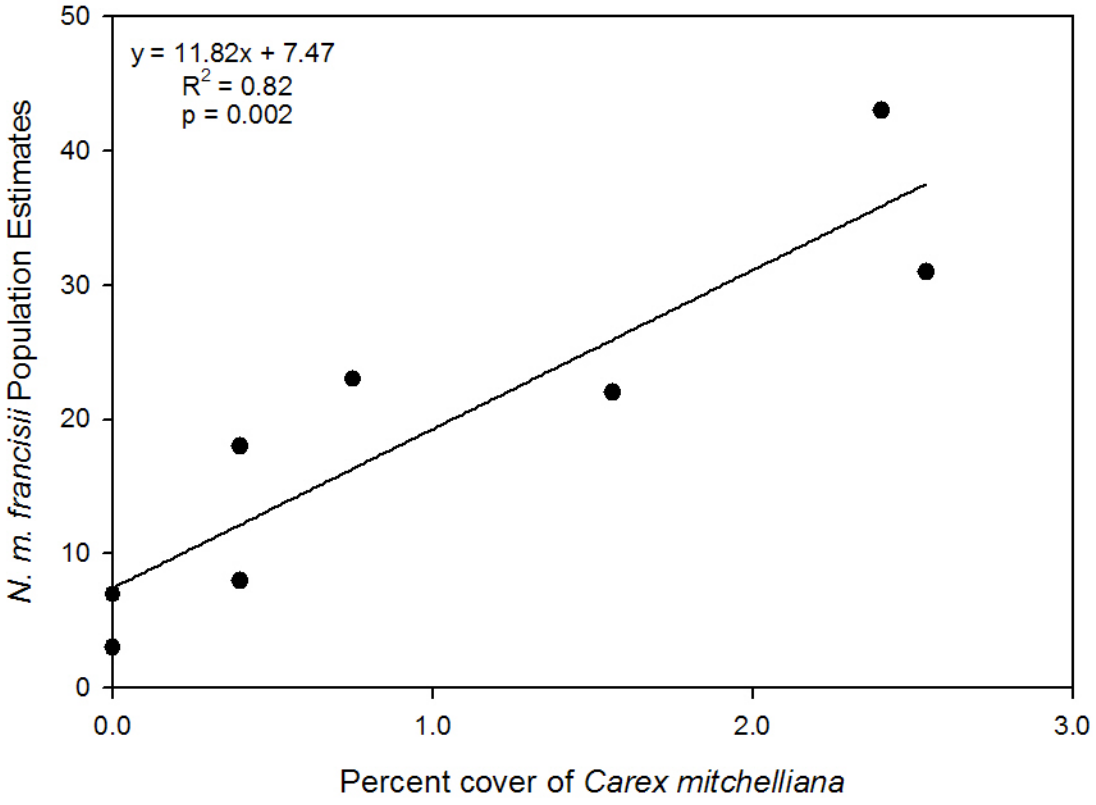

Figure 1.2. Estimates of percent cover of *C. mitchelliana* associated with butterfly abundance estimates using data from 1x1 plots from 2005 and 2006.

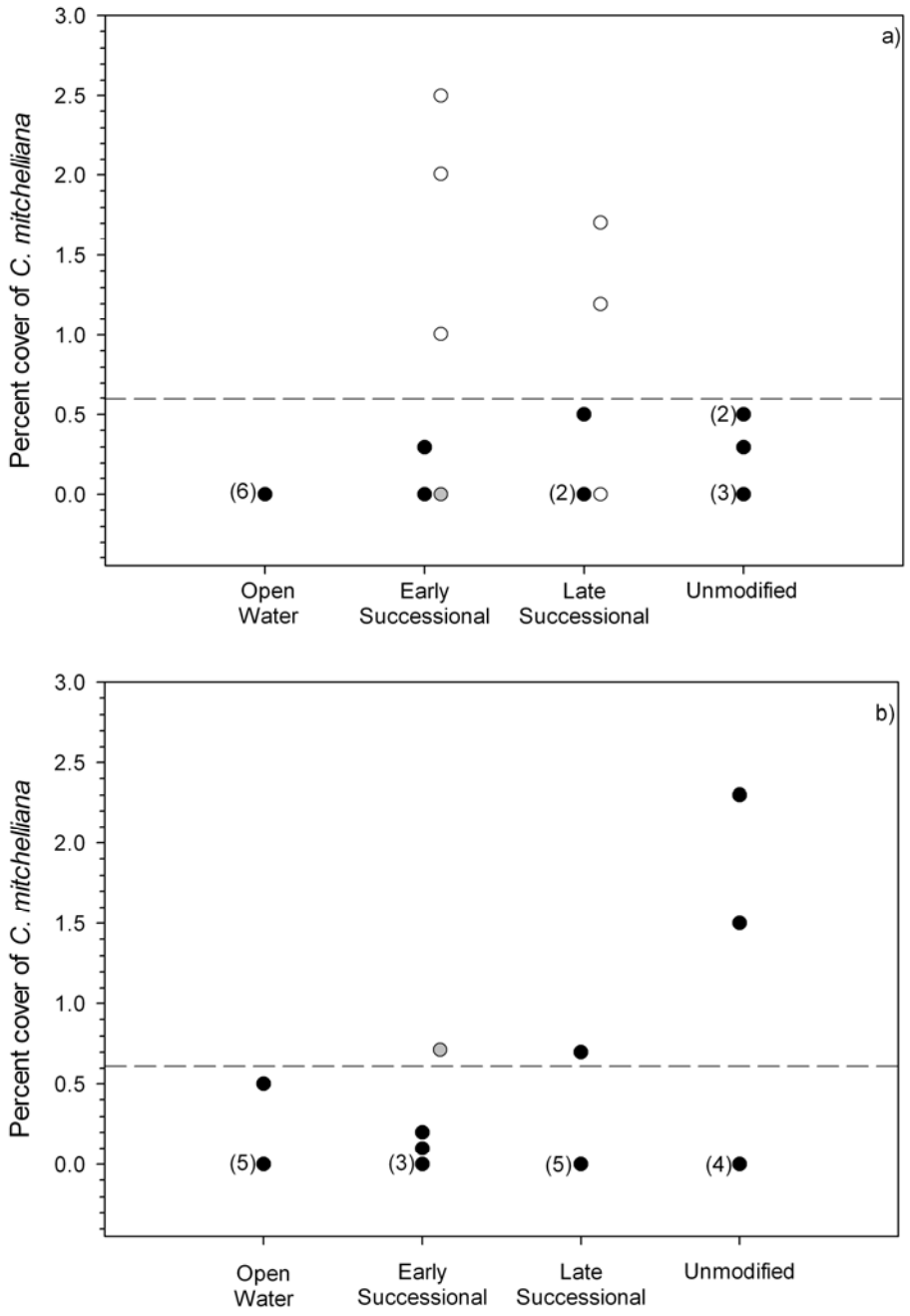

Figure 1.3. Percent cover of *C. mitchelliana* across patch types (N = 12 in each habitat) in stream drainages a) with current *N. m. francisci* subpopulations and b) without current *N. m. francisci* subpopulations. The horizontal line indicates values of percent cover ≥ 0.6%. Offset open circles designate sites recently occupied by *N. m. francisci*. White circles denote currently occupied patches by *N. m. francisci*. Gray circles represent transitory sites or patches where *N. m. francisci* populations went extinct. Black circles indicate patches unoccupied by *N. m. francisci*. The numbers in parentheses show the number of patches with a given value of percent cover of *C. mitchelliana*.

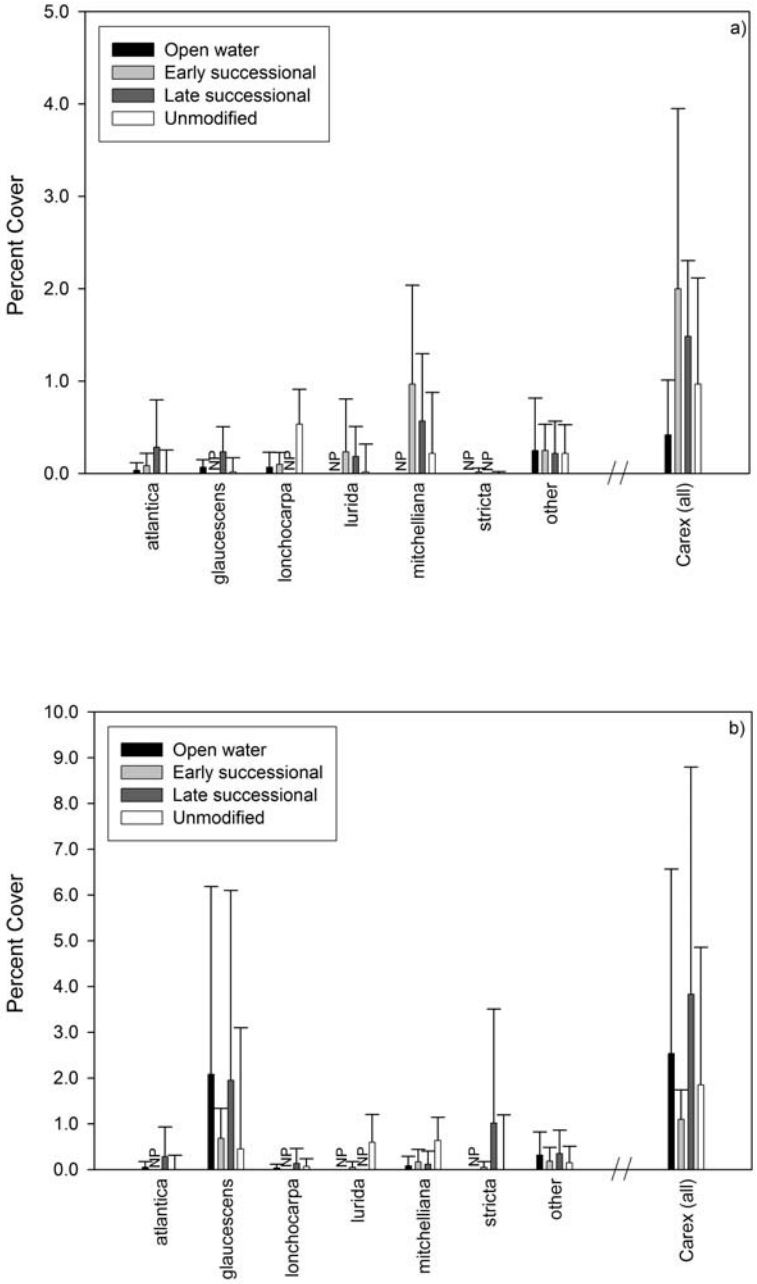

Figure 1.4. Percent cover of *Carex* across four different habitat types in stream drainages a) with current *N. m. francisci* subpopulations (D, E) and b) without current *N. m. francisci* subpopulations (C, I). NP denotes incidences of plant never present in a given habitat type. Error bars represent ± 1 standard error.

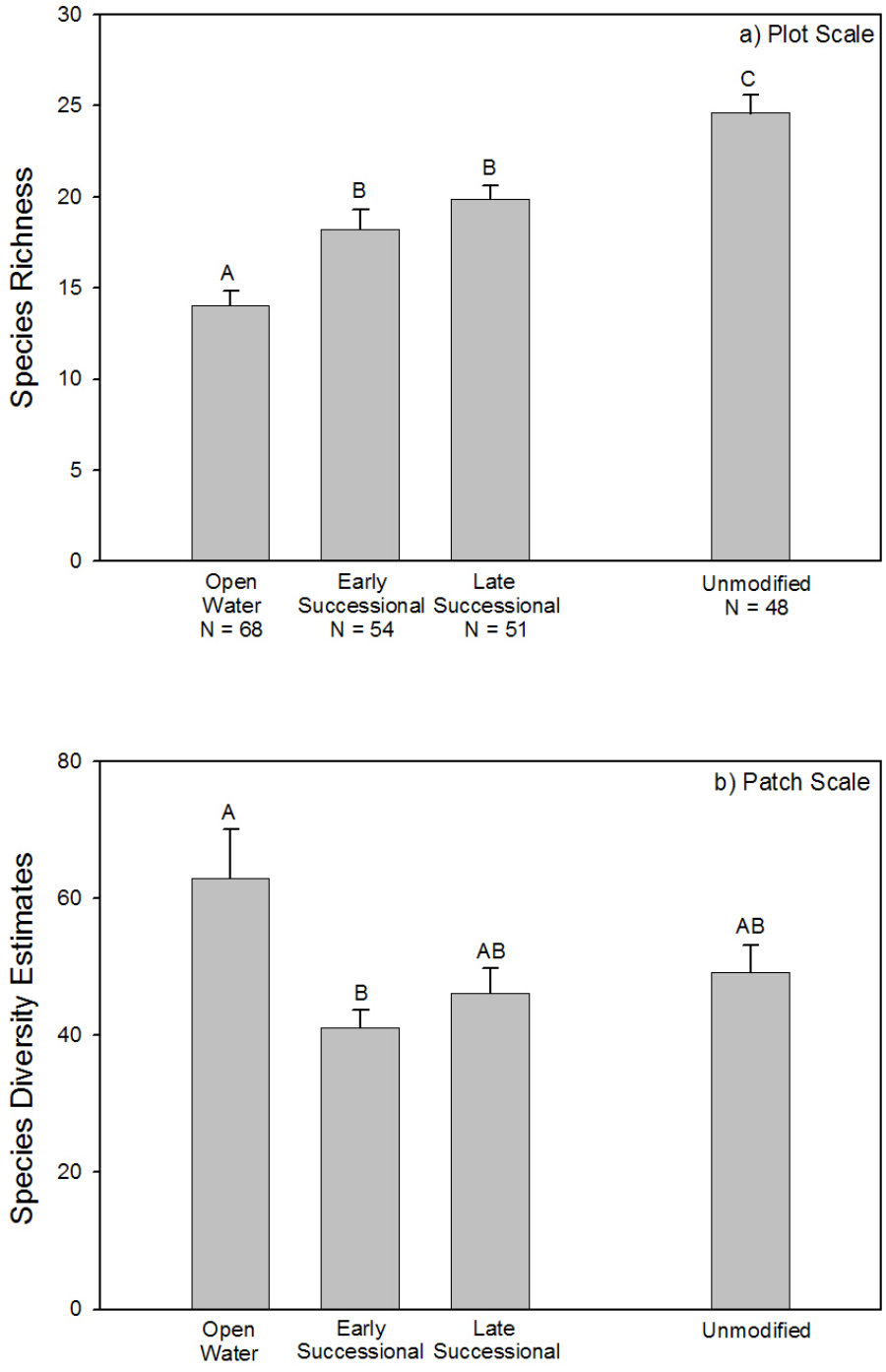

Figure 1.5. Species richness by habitat type at a) plot scale (N = 219) and b) patch scale (N = 48). Error bars represent +1 standard error. Bars with different letters are statistically significantly different at an experimental error rate of $p < 0.05$ using a Tukey test for multiple comparisons.

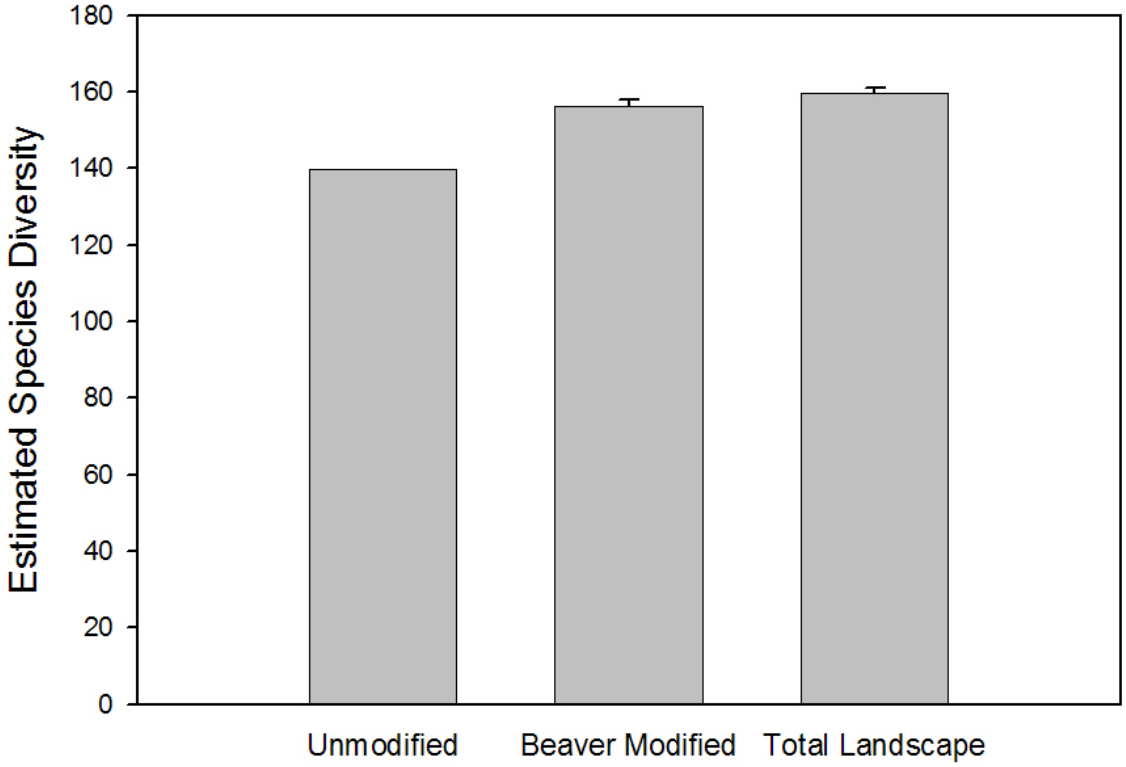

Figure 1.6. Estimated species diversity of simulated landscapes composed of unmodified plots, beaver-modified plots, or of the total landscape (both unmodified and beaver-modified plots). Error bars represent ± 1 standard error.

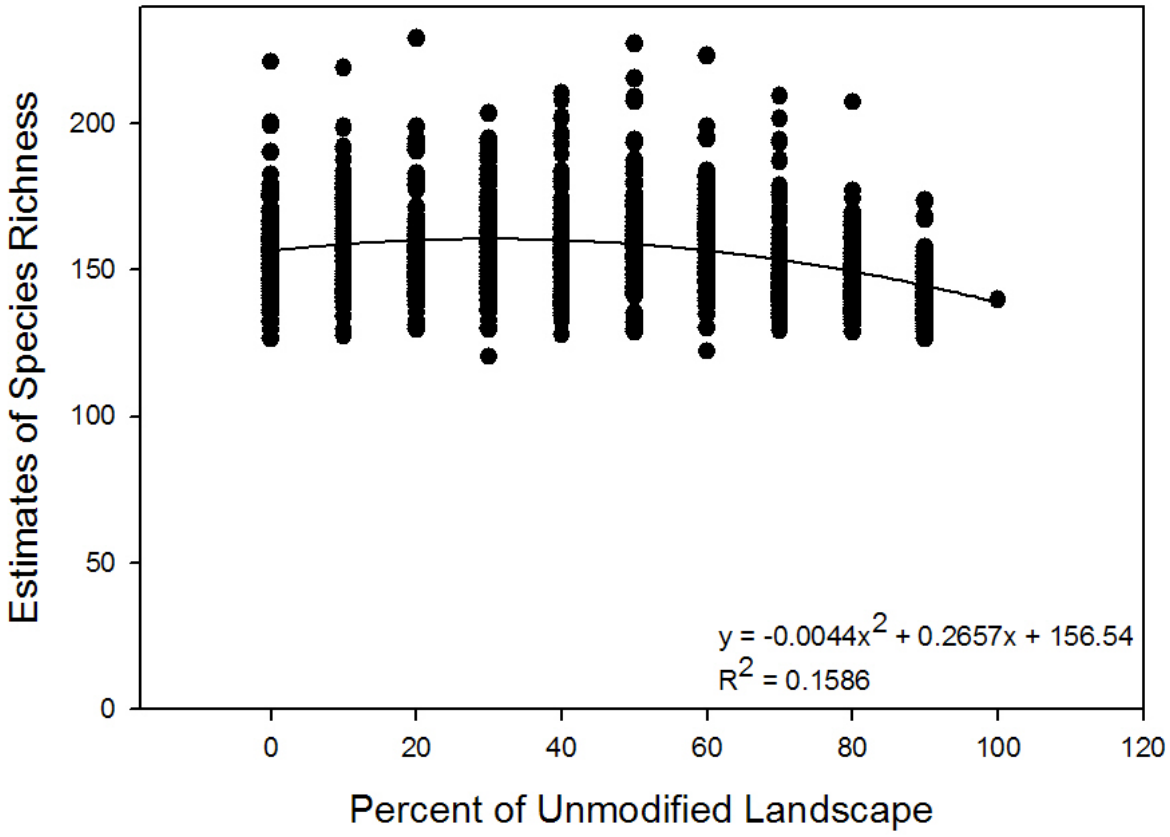

Figure 1.7. The relationship between the proportion of unmodified habitat in the landscape and estimated species diversity.

CHAPTER 2: EFFECTS OF DISTURBANCE ON METAPOPULATION SIZE IN SUCCESSIONAL LANDSCAPES

A paper submitted to *Landscape Ecology*

Rebecca A. Bartel, Brandon J. Puckett, and Nick M. Haddad

Abstract

Classic metapopulation models assume a static landscape. Yet many habitats are dynamic with patches of varying suitability distributed across the landscape. Metapopulation dynamics may depend crucially on habitat dynamics caused by disturbance and succession. While recent models have examined effects of disturbance on metapopulation size, my work is the first to evaluate impacts across different series of succession. To assess how landscape and species' characteristics affect metapopulation size, I used a spatially implicit patch transition model. I analyzed the effects of varying disturbance frequencies (low, moderate, and high) in different rates of successional speed (fast, medium, slow) to cover much of the biological range of species' response. To assess how species sensitivity to habitat changes respond to shifting patch availability across the landscape, I compared three occupancy rules, which determined which successional stage was suitable for occupation (early, late, or all habitats), and a range of colonization rates. While my models attempted to explore general trends in metapopulation dynamics in successional landscapes, I was also motivated by the application of the results to a critically rare species of butterfly dependent on successional habitats, the St. Francis satyr, *Neonympha mitchellii francisci*. I demonstrate that metapopulation size is influenced by a combination of factors including the speed of succession, disturbance frequency, when patches are occupied (i.e., early or late successional

stages), and colonization rate. In general, I found that metapopulation size increased with rate of succession. I also detected an interaction between disturbance frequency and occupancy rules, where higher levels of disturbance in early successional habitats and lower levels of disturbance in late successional habitats resulted in increased metapopulation sizes. Knowledge of successional speed and colonization rates can determine whether conservation strategies should concentrate on modifying landscape structure or habitat quality. Through evaluating how species respond to environmental changes across different models of disturbance and succession, I can make better conservation and management recommendations for rare species which utilize successional habitats.

Introduction

Classical metapopulation theory assumes that the persistence of populations depend on their existence as a set of independent local subpopulations connected across the landscape through migration (Levins 1969, Harrison and Taylor 1997). Until recently, metapopulation theory presumed a static landscape. However, many habitats are dynamic, and disturbance and succession may influence metapopulation size more than population dynamics within subpopulations (Harrison and Taylor 1997, Hanski 1999, Thomas and Hanksi 2004). In the classic Levins (1969) model, a threshold of (re-)colonization is necessary for metapopulation persistence, above which patch occupancy can reach equilibrium as empty patches that go locally extinct are colonized. Non-equilibrium metapopulations can take place when species sensitive to specific habitat characteristics are dependent on succession and disturbance (Thomas and Hanski 2004). By simulating a

landscape with a dynamic distribution of suitable and unsuitable habitats, I evaluate how varying disturbance rates in different scenarios of succession affect metapopulation size, defined here as the number of patches occupied in the landscape, for species in which colonization and extinction rates are affected by habitat changes.

Contrary to classical metapopulation theory, patches, or discrete areas of habitat, across the landscape are not always equal in suitability and the suitability of a given patch can vary temporally. Metapopulation size and persistence may depend crucially on habitat dynamics caused by disturbance and succession (Harrison and Taylor 1997, Thomas and Hanski 2004, Snäll et al. 2005, Wilcox et al. 2006, Vuilluemier et al. 2007). Changes in habitat can result from habitat loss or fragmentation (Nee and May 1992, Purves and Dushoff 2005) or through vegetative succession (Paine and Levin 1981, Harrison 1994, Harrison and Taylor 1997, Stelter et al.1997). As succession continues, patches can convert from suitable to unsuitable habitats, or vice versa. The longer time patches remain unsuitable, the lower is expected metapopulation size (Ellner and Fussman 2003, Wilcox et al. 2006). Disturbance can reset succession and either destroy suitable patches or convert sites to empty suitable patches that are available for colonization (Amarasekare and Possingham 2001). Several recent models examine the effects of disturbance on metapopulation dynamics (Johnson 2000, Hastings 2003, Wilcox et al. 2006, Ross et al. 2008), but all of these studies evaluate processes in the context of a single type of succession. Here, I assess how disturbance frequency interacts with rates of succession by observing metapopulation dynamics over different scenarios of succession speed.

Temporal and spatial structure of habitat patch destruction can impact metapopulation size and persistence (Johnson 2000, Amarasekare and Possingham 2001, Johst and Drechsler 2003, Wilcox et al. 2006). In cases where species occupy habitat patches in early or mid-successional stages, succession can eliminate previously available patches (Menges 1990, Warren 1991, Thomas 1994) and cause extrinsic habitat dynamics, rather than intrinsic processes of colonization and extinction, to dominate metapopulation dynamics (Wahlberg et al. 2002, Thomas 1994). When species depend on late successional stages, disturbance can also destroy existing suitable habitat patches (Gutiérrez and Harrison 1996, Walters et al. 2002). By decreasing patch occupancy rates, disturbance can increase local extinction rates both directly by converting suitable habitat patches to unsuitable patches, and indirectly by reducing the proportion of empty patches that could be colonized (Thomas and Hanski 2004, Vuilluemier et al. 2007). Most successional metapopulation models assume suitable habitats exist in one stage (e.g., early or late) of succession (Johnson 2000, Ellner and Fussman, 2003, Hastings 2003, Wilcox et al. 2006). I examine impacts of disturbance and succession over a broader range of scenarios to investigate what landscape and species traits ultimately determine metapopulation size.

The proportion of a landscape a species occupies is dependent on the rate of habitat change and colonization (Johnson 2000, Amarasekare and Possingham 2001, Ellner and Fussman 2003, Wilcox et al. 2006). The probability of colonization of available suitable habitat increases with connectivity to existing subpopulations (Hanksi 1999), more likely occurring between adjacent patches (Harrison 1991, Wiens 2001, Molianen and Hanski 2001, Vuillemier et al. 2007). Therefore, movement of individuals can affect metapopulation

dynamics (Hanksi and Ovaskainen 2000, Johnst et al. 2002, Vuilleumier et al. 2007). When patch connectivity is high, one effective management strategy for increasing metapopulation persistence is to increase colonization rates (Vuillemier et al. 2007). Because species may need to colonize habitat patches at rates higher than the succession rate converting suitable sites to unsuitable habitat to avoid local extinctions (Snäll et al. 2005), I assessed how metapopulation size was related to a broad range of colonization rates.

Rare species with smaller population levels can be particularly sensitive to subtle changes in habitat dynamics (Harrison 1991, 1994). The assumption of balanced extinction-colonization dynamics in classical metapopulation models (Levins 1969) has been questioned in the context of rare and endangered species (Harrison 1991, 1994, Thomas 1994). If the cause of extinction is a deterministic population response to unsuitable habitat conditions, it is possible that habitat patches may remain unsuitable and unavailable for recolonization even after local extinction of some patches (Thomas 1994, Ovaskainen and Hanski 2004). Following a natural disturbance or anthropogenic alteration of habitat, species colonize specific successional stages and then populations of future generations are reduced through continued succession. This has been best documented in European butterflies (Warren 1991, Thomas 1994, see Thomas and Hanski 2004 for review), but there are numerous critically rare and endangered species whose populations respond to habitat requirements of specific successional states (Menges 1990, Gyllenberg and Hanski 1992, Pulliam et al. 1992, Gutiérrez and Harrison 1996, Walters et al. 2002, Ch. 1). Yet, despite increasing evidence of rare species that track habitat dynamics, there are few applications of successional metapopulation models with species of conservation concern (see exceptions Wahlberg et al.

2002, Ross et al. 2008). I assess how patch colonization and occupancy patterns in successional landscapes may differ in smaller metapopulations that are often observed in rare species.

To evaluate how landscape and species' characteristics affect metapopulation size (i.e., number of occupied patches in the landscape), I used a spatially implicit patch transition model. Specifically, I analyzed the effects of varying disturbance frequencies (low, moderate, and high) in different scenarios of succession. Because I are interested in general trends of metapopulation size to dynamic distributions of suitable habitat, I use three different models of successional rates (fast, medium, slow) to cover the biological range of species' response. To assess how species sensitivity to habitat changes respond to shifting patch availability across the landscape, I compare three occupancy rules (early, late, or all habitats) and a range of colonization rates. Additionally, I was interested in how species management can be affected, given different distributions of suitable habitat patches for occupation. While my models attempt to explore general trends in metapopulation dynamics in successional landscapes, I was also motivated by the application of the results to a critically rare species of butterfly dependent on successional habitats.

Methods

Model structure

To examine the effects of varying disturbance and length of succession on metapopulation size, I constructed a Markov transition matrix, similar to that of Johnson (2000) (1). I define succession here as predictable change in community structure over time,

presented here as a gradient of different stages (e.g., early and late succession). Columns of the matrix represent the patch state at the current time (t), and rows represent the patch state at the next time step ($t + 1$). Entries in the first row contain the disturbance rate, d, for each stage. I assumed that some stages were more suitable than others given the species of interest. For example, late successional habitat would be unsuitable for a species that prefers early successional habitat. I also assumed that once disturbed, patches became unsuitable until they succeeded into a suitable stage. Once a proportion of patches in a given stage are disturbed, they are converted back to the initial stage and succession is reset. The remaining rows contain the transition probabilities of succeeding from one stage to another, s, which is equal to 1-d. Each stage is forced to move through the successional series at rate s, or otherwise is disturbed. Unless disturbed, only the final stage is allowed to remain in its current state, similar to a climax successional stage. Therefore, when only early successional stages are suitable, species could reach extinction through disturbance or if the patch succeeds to an unsuitable stage (e.g., late successional). When only late successional stages are suitable, extinction can only occur through disturbance.

$$\begin{bmatrix} d_1 & d_2 & d_3 & \cdots & d_{m-1} & d_m \\ s_2 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_3 & 0 & \cdots & 0 & 0 \\ 0 & 0 & s_4 & \cdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & s_{m-1} & s_m \end{bmatrix}. \quad (1)$$

To observe how effects on metapopulation size vary with different succession scenarios, I used three different models with various succession speeds: 1) fast succession

with four stages, 2) moderate succession with 20 stages, and 3) slow succession with 100 stages. I chose these three models as examples which extend across the biological range of successional values. Using an annual time step, these three models allow me to investigate disturbance and successional dynamics across a spectrum of realistic scenarios. Fast succession is analogous to shortgrass prairie fires with a recovery time of four years (Bragg 1995). Moderate succession is comparable to disturbed systems such as beaver impoundments or sand dune formation (Cowles 1899, Litcher 1998). Slow succession is equivalent to longer successional series such as recovery of a forest ecosystem after a fire (Romme and Despain 1989, Turner et al. 1994).

Model parameterization

An m by m transition matrix, A, was parameterized for each succession model, where m is equal to the number of stages. Each succession model was iterated over 50 time steps. I found this was a reasonable amount of time to observe model dynamics and reach stable stage distribution. To examine how metapopulation dynamics were affected by different disturbance regimes, I varied values of d to test for the effects of three different levels of disturbance intensity: low, moderate, and high. In a given simulation, I set the disturbance rate to be equal across all stages ($d_1 = d_2 = d_m$). Disturbance rates were equal across stages as a reasonable simplification is that the probability of any stage experiencing a perturbation was the same. To evaluate the effects of varying disturbance frequencies on metapopulation dynamics, I chose three values to represent a range of biologically meaningful scenarios of low, moderate, and high levels of disturbance. In the fast succession

model, *d* was equal to 0.2, 0.4, and 0.7 for low, moderate, and high levels, respectively. For the other models, I scaled measures of *d* in proportion to the increase in number of stages. For example, $d = 0.2$ at low disturbance intensity in fast (4 stages) models; subsequent values of disturbance for moderate (20 stages) and high (100 stages) models of succession were divided by five and 25 respectively (see Table 2.1 for all parameter values).

To evaluate how species could respond to shifting patch availability across the landscape, I varied occupancy rules and colonization rates similarly for all successional models. An occupancy rule dictated which stage or stages could be occupied across the landscape, while occupancy rates are defined by the probability by which a patch is colonized. Occupancy could be in 1) all patches, similar to the classic Levins (1969) model which assumes patch occupancy is equally distributed among patch types, 2) early successional patches only, or 3) late successional patches only (see Table 2.1 for all models). When all stages were allowed to be occupied, every stage except for the initial disturbed stage in each model was available for colonization. In cases where species could occupy only one type of habitat (e.g., early succession), 25% of all stages were available for colonization (see Table 2.1 for specific stages in each model). I also varied colonization rates, *c*, and tested values of 0.1, 0.25, 0.5, 0.75, and 0.9 to span the majority of the possible range and values.

Stage vectors for each succession model contained 2500 patches in the landscape. This number allowed me to examine habitat dynamics with a moderate number of patches in each stage. The entire landscape was composed of habitat patches, and there are no cells species may not occupy when suitable given occupancy rules. At the beginning of model

runs, each stage contained 625, 125, or 25 patches for the fast, medium, and slow succession models respectively. At each time step, I multiplied the transition matrix, *A*, by the current stage vector, *r*, to generate the next distribution of stages. I determined the stable patch distribution by calculating the right eigenvector and observing the proportions of patches in each stage, P_{stage} (see Appendix B for all variables).

In order to assess whether a patch was suitable to be occupied, I followed patches at each stage through time. To track the proportion of each stage, I calculated the number of disturbed patches by multiplying *r* by the first row of *A*, which contained the disturbance rates for each stage. For all stages I then assessed the number of patches that succeeded to the next stage. Once I estimated how many patches in a given stage were disturbed or succeeded to the next stage, I examined how many patches remained in the stage they started in. In the fast succession model, all patches were disturbed or forced to move to the next stage type (i.e., early successional), which was different than the current stage. As a result, patches could only remain in the last stage. In the other succession models, stages could continue to be in the same stage type (i.e., early successional) because there were several consecutive stages of that type.

After determining the fate of patches for all stages, I assessed whether patches were occupied or vacant. The number of currently occupied patches was calculated as patches that could be occupied given the occupancy rule multiplied by the proportion of available patches that could be occupied that remain in each stage. When disturbance or succeeding to an unsuitable stage resulted in all patches being unsuitable, then no current occupants persisted. I estimated the number of patches with new arrivals by the product of the number of patches

that could be occupied given the occupancy rule, the proportion of unoccupied patches available on the landscape, and the colonization rate, c. The total quantity of occupied patches, O_{total}, was the sum of current occupants that survived disturbance and succession and the number of new colonists. I estimated the total proportion of landscape occupied, P_{total}, by dividing O_{total} by the total number of patches in landscape.

To test the role of stochastic fluctuation in changes in metapopulation size, I added variation to disturbance rates in the models by selecting values of d from a uniform random distribution with maximum variance of 50 percent of d. In cases where this could result in stochastic value of $d > 1.0$, I truncated values at 0.99. Stochastic models were assessed for a subset of the models with the median occupancy rate, $c = 0.5$. I calculated the mean and standard deviation for 100 trials for each model and observed if increasing variation caused an increase or reduction of occupancy relative to the deterministic models.

Although my work is meant to be a general exploration of the effects of disturbance and succession on metapopulations, I was initially motivated by one rare species, the endangered St. Francis' satyr butterfly, *Neonympha mitchellii francisci*. The known population of *N. m. francisci* ranges between 700-1400 adult individuals, with their global distribution limited to small patches of habitat (~30 ha) in central North Carolina (Kuefler et al. 2008). Several subpopulations of butterflies exist in early successional riparian habitat patches which often contain their presumed larval host plants, *Carex* spp. (Kuefler et al. 2008, Ch.1). Multiple subpopulations comprise a metapopulation in a single watershed and a network of watersheds connects the rangewide population (Kuefler et al. 2008). These habitat patches are created and maintained by beaver (*Castor canadensis*) through dam-

building and the resulting flooding and initiation of vegetative succession (Ch.1). These riparian meadows succeed to woody vegetation within 10-20 years, becoming unsuitable for butterfly occupation (Kuefler et al. 2008). Because the spatial distribution of *N. m. francisci* is limited like that of many rare species, I also tested models which reduced overall landscape size from 2500 total patches to 60 patches, initially with 3 patches in each stage. Using this modification, I compared how rates of succession and disturbance frequency could impact smaller metapopulations to other models with larger landscapes.

In addition to the rules above, the context of metapopulations of *N. m. francisci* is different because disturbance is persistent and not an isolated event as observed in natural disturbances such as hurricanes or wildfires. I found the assumption of equal susceptibility of patches to disturbance was unrealistic (Ross et al. 2008) in this case and modified models accordingly to examine how disturbance and variable occupancy rules and rates impact rare species. To assess how metapopulation size changes in a rare species sensitive to changing habitats, I customized my original moderate successional model. Since wetland meadows succeed to riparian forest in approximately 20 years, I kept the successional speed the same. Because beaver ponds can remain disturbed and typically are not abandoned after one year, I allowed the disturbance rate of the initial stage to be higher than other d values ($d_1 \neq d_2$; $d_2 = d_3 = d_m$). I tested the impacts of two possible disturbance rates for the initial stage, d_1, by adding 0.5 or 0.75 to each original d value given disturbance frequency. This allowed evaluation of ponds that remained disturbed for various amounts of time as I observe in the field.

Results

I found proportions of disturbed habitat in the landscape decreased and of early successional habitats increased from fast to slow succession models for all disturbance frequencies. Simulated landscapes had similar amounts of late successional habitat regardless of successional rate. In general, the proportion of the landscape occupied increased as the length of succession increased. When early successional habitats were suitable, metapopulation size increased with increasing disturbance frequency for moderate and slow successional models (Figure 2.1a). Medium frequencies of disturbance produced the highest metapopulation persistence in fast succession models. When late successional habitats were suitable, the total proportion of landscape occupied decreased with increasing disturbance regardless of the rate of succession (Figure 2.1b). With medium and high levels of disturbance, models of slow succession occupied larger proportions of the landscape, while moderate succession resulted in the most occupied stages at low disturbance levels (Figure 2.1b). When all stages could be occupied, I found that almost the entire landscape was occupied in moderate and slow succession models, decreasing slightly with increasing disturbance level (Figure 2.1c). Yet, even though the majority of the landscape consisted of suitable habitat, metapopulation sizes in fast models of succession decreased with increasing disturbance (Figure 2.1c).

I also detected interactions among successional speed, disturbance, occupancy rules, and colonization rate (Figure 2.2). In all scenarios, I found that increasing colonization rates (c) resulted in higher proportions of landscape occupied. In the fast succession models, I found increasing the colonization rate from 0.1 to 0.9 resulted in the highest increases in

proportion of landscape occupied. This trend was particularly evident when smaller proportions of landscape in the early successional stages were occupied, with increases >400% in proportion of landscape occupied for all disturbance frequencies. When late successional stages were occupied in the fast models, I also detected increases in proportion landscape occupied (range: 145-362% from low to high disturbance frequencies) as colonization rates increased. In the moderate and slow succession models, I found overall proportions of landscape occupied while increasing colonization rates had reduced effects on increases in amount of landscape occupied (range: 4-68%).

After testing the effects of stochastic fluctuation in metapopulation size, I found that adding variation to the models did not alter trends detected in the deterministic models of any succession scenario.

By modifying the moderate succession model to mimic the effects of beaver disturbance on habitat suitability for a rare butterfly, I found that increasing the probability of a pond remaining disturbed resulted in differences in occupancy trends for any level of disturbance, with larger deviations from the original model observed with higher increases in disturbance rate (Figure 2.3). By changing the disturbance rate by 0.75, I found total metapopulation size was always reduced compared to other scenarios. These differences were most notable when early successional or all habitat could be occupied (Figures 2.3a and 2.3c). When species occupied early successional habitats, such as my motivating species, *N. m. francisci* does, smaller proportions of the landscape were colonized with medium and high levels of disturbance in the modified models. Similarly, I found smaller percentages of the

landscape occupied in the modified models when all stages were available for colonization, regardless of disturbance level (Figure 2.3).

Reductions in overall landscape size resulted in similar general trends in metapopulation size to those found in larger landscapes, yet with lower proportions of the landscape occupied (Figure 2.3). Metapopulation sizes increased when species occupied early successional stages and decreased with increasing disturbance frequency (Figure 2.3). When early successional stages were occupied, global extinction occurred in the modified model with the highest initial disturbance value, d_1, with a low frequency of disturbance in models with reduced landscape size (Figure 2.3a). When late stages were occupied, at high levels of disturbance, metapopulations in all models colonized < 10% of the landscape (Figure 2.3b).

Discussion

The assumption of classic metapopulation theory that all patches across the landscape have equal suitability is too simplistic for many real cases that involve rare species. My work is unique in evaluating occupancy rates in different stages of succession. My results support what others have proposed, that many metapopulation processes are driven by habitat dynamics instead of subpopulation processes such as colonization and extinction (Thomas 1994, Harrison and Taylor 1997, Wahlberg et al. 2002, Thomas and Hanski 2004, Wilcox et al. 2006). While recent models have examined effects of disturbance on metapopulation size (Johnson 2000, Hastings 2003, Wilcox et al. 2006, Ross et al. 2008), my work is the first to assess impacts across different lengths of succession. I demonstrated that metapopulation

dynamics are influenced by a combination of factors including the speed of succession, disturbance frequency, when patches are occupied (e.g., early or late successional stages), and colonization rate. In general, I found that metapopulation size increased with length of succession. I also detected an interaction between disturbance frequency and occupancy rules, where higher levels of disturbance in early successional habitats and lower levels of disturbance in late successional habitats resulted in increased metapopulation sizes. Given knowledge of successional speed and disturbance frequency, this may determine whether conservation strategies focus on modifying landscape structure or patch availability (Johnson 2000, Thomas and Hanski 2004, Ross et al. 2008).

Successional speed was important in influencing metapopulation dynamics, yet these effects were related to disturbance frequency and occupancy rules. Overall, I detected a general trend of metapopulation sizes increasing with length of succession. Metapopulation sizes of early occupants in ecosystems with fast succession (~4 years) were highest with medium levels of disturbance, while organisms in ecosystems with moderate (~20 years) or slow (~100 years) models of succession occupied higher proportions of total available suitable habitat with high levels of disturbance. When late or all habitats could be occupied, metapopulation sizes of all succession speeds were highest with low levels of disturbance. Lower levels of disturbance in these scenarios allow species to continue to occupy suitable habitat and avoid extinction through habitat changing into unsuitable disturbed or early successional patches.

Disturbance frequency affected metapopulation size, but the effects of disturbance frequency depended on what successional stages were suitable and could be occupied. For

species that depend on early successional habitats, metapopulation size increased with increasing disturbance frequencies. Examples of occupants of early successional habitats include many rare and endangered plants (Menges 1990, Kaye et al. 1999, Pendergrass et al. 2001), birds (Carlson 2000, Pulliam et al. 1992), and butterflies (see Thomas 1994, Thomas and Hanski 2004 for reviews). Conservation management implications for these situations could be to maintain higher levels of disturbance to provide necessary earlier successional habitats for endangered species.

In contrast to species that occupy early successional habitats, when species favored late successional habitats, lower levels of disturbance increased metapopulation size for all lengths of succession. Examples of some threatened or critically rare occupants of later successional stages are red-cockaded woodpeckers (*Picoides borealis*; Walters et al. 2002) and the northern spotted owl (*Strix occidentalis caurina*; Gutiérrez and Harrison 1996). My results suggest effective conservation and management for late successional occupants would be maintaining low levels of disturbance regardless of successional speed.

When I relaxed the assumption of the classic Levins (1969) model that all habitats are equally suitable for occupation, I found different optimal combinations of disturbance, succession length, and habitat suitability for different sets of species. Metapopulation sizes for early occupants were highest when disturbance was high and succession was slow, whereas metapopulation sizes for late occupants were highest when disturbance was low. While this is biologically realistic, it may not always result in general trends for conservation management of rare species.

I was motivated by the implications of these models for the metapopulation dynamics of a critically rare species of butterfly dependent on successional habitats. Model simulations suggested higher proportions of the landscape were occupied by butterflies with high levels of disturbance. Unlike many natural disturbances such as fire or hurricanes, the disturbance created by beavers is persistent and not an isolated event. I found modification of the disturbance rate for the single initial stage affected the overall proportion of landscape colonized by the butterflies. Reduced landscape size further exaggerated observed differences in species response to disturbance frequencies. For early successional occupants such as *N. m. francisci* with limited spatial distributions (<30 total ha of habitat occupied), reduced landscape size would have consequences of global extinction in scenarios of low overall levels of disturbance combined with beaver pond persistence. Subpopulations in habitats with the highest likelihood of remaining disturbed were driven to global extinctions. Managing beaver populations to promote higher levels of disturbance while creating a complex spatial landscape structure of both disturbed and suitable habitats should increase *N. m. francisci* metapopulation sizes.

Colonization rates impacted metapopulation size, but the effects of changing colonization rates were contingent on rates of succession and which successional stages could be occupied. For both early and late occupants in systems with fast succession, increased colonization rates dramatically increased metapopulation size. Increasing connectivity with stepping stones or corridors to create habitat networks that aid movement can alleviate risks of extinctions for some metapopulations (Hanksi 1999, Snäll et al 2003, 2005). In these cases, species must colonize habitat patches at a rate higher than succession

converts suitable patches to unsuitable patches (Snäll et al. 2005). For all occupants in moderate and slow succession, regardless of which stage could be occupied, colonization rates did not seem to substantially increase occupied proportions of landscape. This would suggest that increasing habitat quality would have a greater effect than increasing connectivity in these scenarios.

While facilitating some movement between patches is necessary, my results suggest management strategies that increase habitat quality may be most successful for early successional species with moderate speeds of succession such as *N. m. francisci*. Patch quality and composition of habitat patches may be related to presence of host plant species ("colonization effect"; Kuussaari et al. 2000, Hanski and Singer 2001, Hanski and Heino 2003). *N. m. francisci* occupancy is correlated with the presence and abundance of presumed host plants (Ch. 1). Local extinctions also can be a consequence of gradual reduction in patch quality which can deterministically cause population declines (Paine and Levin 1981, Stelter et al. 1997, Snäll et al. 2003). Additionally, extinction debt can follow habitat loss if threshold conditions for survival are no longer met for some species, but they have not gone extinct yet because of the time delay in response to environmental change (Tilman et al. 1994). This phenomenon can be further exaggerated when rare species populations are already close to extinction thresholds following habitat loss or fragmentation (Hanski and Ovaskainen 2002, Bulman et al. 2007).

A metapopulation approach can be used to identify areas of a fragmented landscape that are closest to extinction thresholds and identify how patch occupancy rates could be altered through managing landscape structure (Thomas and Hanski 2004). Yet, several

caveats exist with using the metapopulation approach for rare species. One of the more fundamental issues is distinguishing habitat and non-habitat, and delineating what is suitable habitat for rare species (Hanski and Simberloff 1997, Bourg et al. 2005, Early et al. 2008, Ch. 3). Additionally, the distribution of suitable habitat does not remain constant though time, particularly for species that track the distribution of successional habitats (Harrison 1991, Thomas 1994, Thomas and Hanksi 2004). Metapopulation models can be applied to these systems when knowledge exists for how the patch network has changed across the landscape or by using predictive habitat models incorporating these changes in spatial structure (Ch. 3).

I have demonstrated the importance of evaluating consequences of habitat dynamics on metapopulation persistence. Disturbance frequency and which successional stages could be occupied strongly affect metapopulation size. Knowledge of successional speed and colonization rates can determine whether conservation strategies should concentrate on modifying landscape structure or habitat quality. Through assessing how species respond to environmental changes across different models of disturbance and succession, I can make better conservation and management recommendations for an endangered species that utilizes successional habitats. While there are limitations of these general metapopulation approaches, simulation models can be combined with niche-based habitat models and field-based methods to further formulate a comprehensive management strategy. Through the continued development and parameterization of models using empirical data for an endangered metapopulation, I can successfully apply patch tracking models to realistic conservation scenarios.

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Table 2.1. Parameters for deterministic simulations of different succession models. All models contain 2500 total patches in the landscape. In cases where species could occupy only one type of habitat (e.g., early succession), 25% of all stages were available for colonization.

Succession model	# of stages	Initial # of patches in each stage	Stages occupied given occupancy rule	*d*	*s*
Fast	4	625	Early = Stage 2	Low = 0.2	0.8
			Late = Stage 4	Medium = 0.4	0.6
			All = Stages 2-4	High = 0.7	0.3
Moderate	20	125	Early = Stages 2-6	Low = 0.04	0.96
			Late = Stages 16-20	Medium = 0.08	0.92
			All = Stages 2-20	High = 0.14	0.86
Slow	100	25	Early = Stages 2-25	Low = 0.008	0.992
			Late = Stages 76-100	Medium = 0.016	0.984
			All = Stages 2-100	High = 0.028	0.972

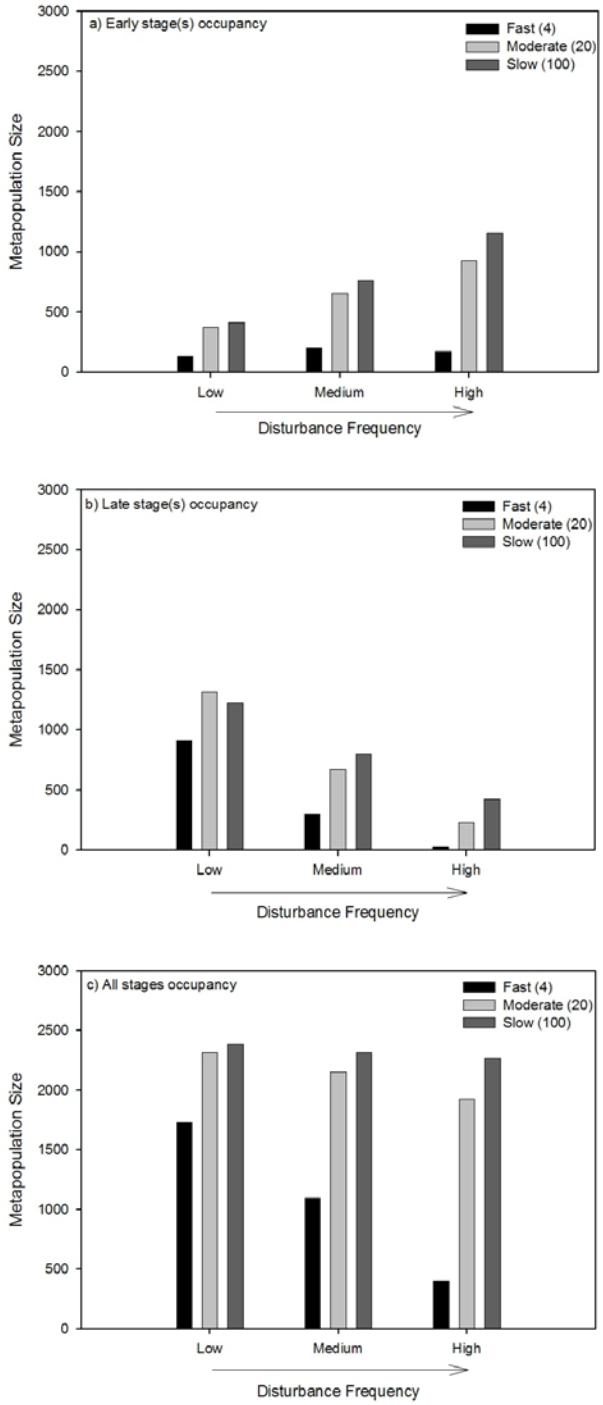


Figure 2.1.Metapopulation size across disturbance regimes for three deterministic succession models (c = 0.5) for three different occupancy rules: a) only early successional habitats, b) only late successional habitats, and c) all stages excluding the initial disturbed stage. Landscape has 2500 patches total.

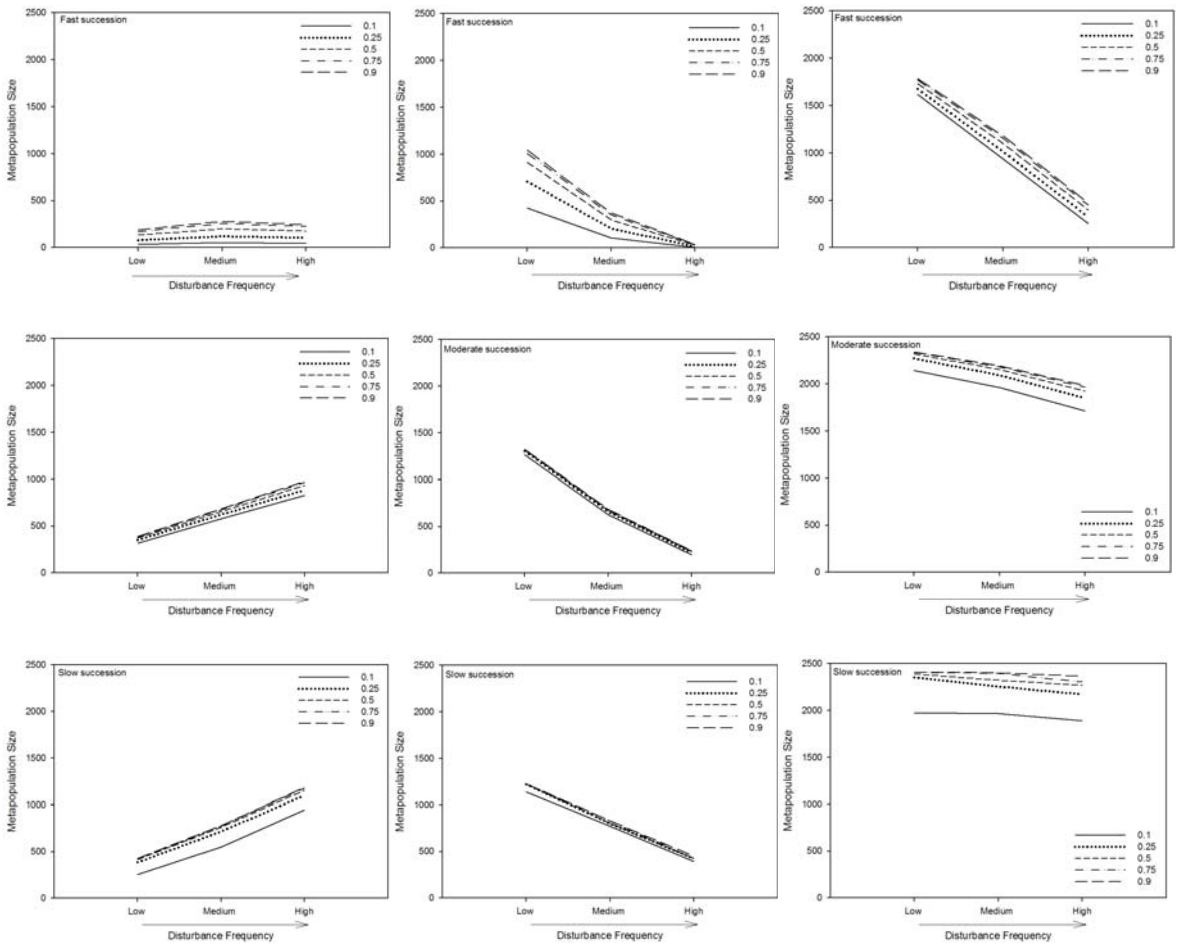
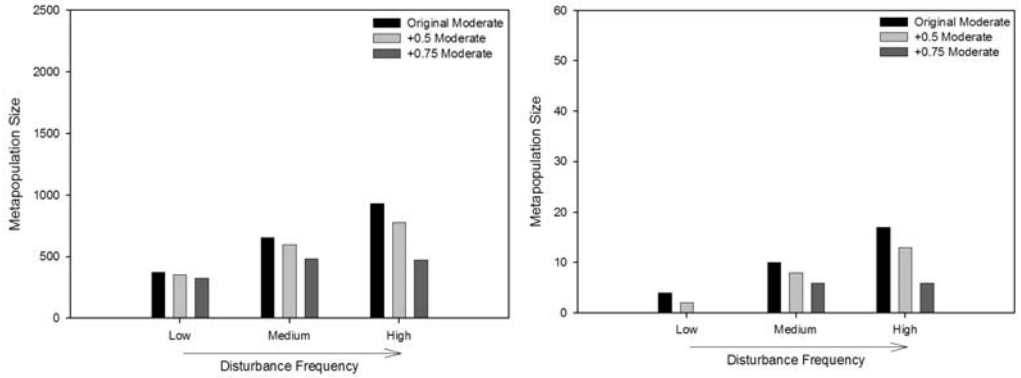
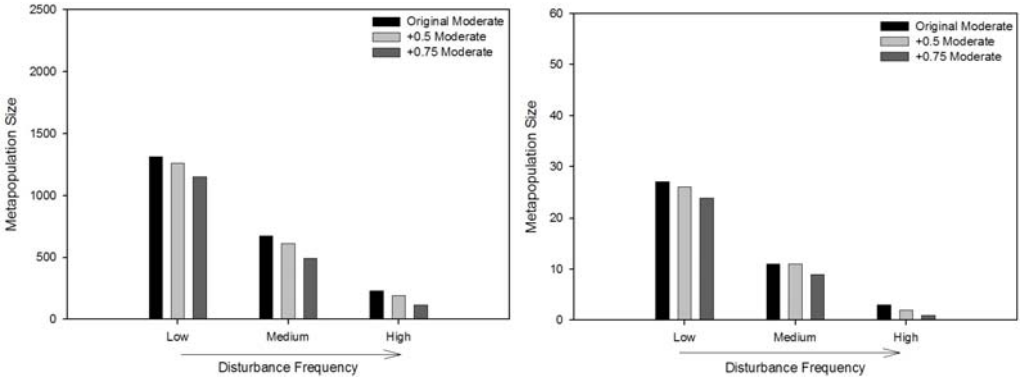


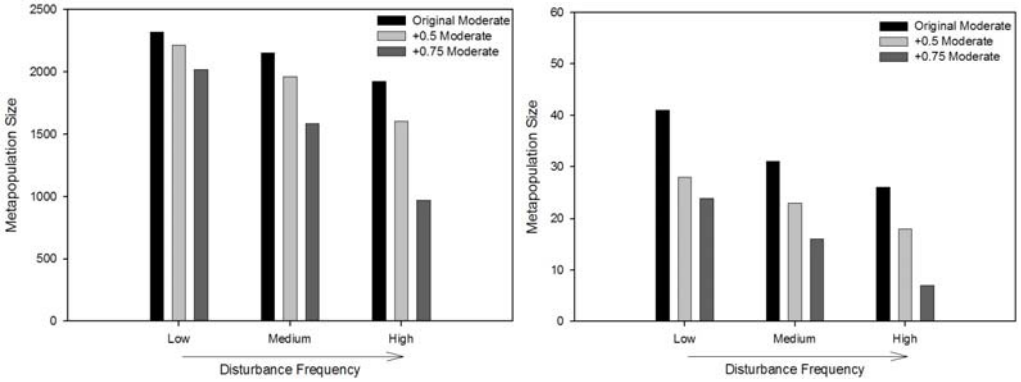
Figure 2.2. Metapopulation size across disturbance regimes for all deterministic succession models for three different occupancy rules: only early successional habitats, only late successional habitats, and all stages excluding the initial disturbed stage, given five different colonization rates (0.1, 0.25, 0.5, 0.75, and 0.9). Landscape has 2500 patches total.



a) Early stage(s) occupancy



b) Late stage(s) occupancy



c) All stage(s) occupancy

Landscape size = 2500 patches Landscape size = 60 patches

Figure 2.3. Metapopulation sizes across disturbance regimes for three moderate succession models (*c* = 0.5) for three different occupancy rules: a) only early successional habitats, b) only late successional habitats, and c) all stages excluding the initial disturbed stage, given two landscapes sizes (2500 or 60 patches).

CH. 3 MONITORING HABITAT DYNAMICS OF RARE SPECIES USING A TIME SERIES OF SATELLITE IMAGES

A paper submitted to *Ecography*

Rebecca A. Bartel and Joseph O. Sexton

Abstract

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. I used field measurements of species occurrence, a 22-year 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. I 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 species 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.

Introduction

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, Latimer et al. 2006).

Species distribution models approximate a species' environmental niche (Hutchinson 1957, Guisan and Zimmerman 2000), 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 (Ferrier 2002, 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 (Guisan and Thuiller 2005, Early et al. 2008). 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, Shelden et al. 2001); yet this information is often missing from species recovery plans (Foin et al. 1998, Crouse et al. 2002, Hoekstra et al. 2002).

I show how habitat models can predict the potential distribution of rare species over time to guide recovery efforts. As a case study, I 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. I use a 22-year series of calibrated 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 though field surveys, I monitored temporal changes in habitat over the study area and used the projections to target sites for reintroduction efforts.

Methods

Study Area

Populations of *N. m. francisci* are known only to exist in south central North Carolina (USA), on Ft. Bragg military reservation (latitude 35°07′30′ N, longitude 79°08′30′ W), which is located on Department 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 approximately 65,032 hectares.

Populations of *N. m. francisci* range between 700-1400 adult individuals for all accessible areas (Kuefler et al. 2008) that are not within military artillery areas. The butterflies occur in several subpopulations in early successional riparian vegetation containing their presumed host plants, *Carex* species (Kuefler et al. 2008). 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 (Ch. 1). 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 sites on five different watersheds within inaccessible military training areas, where activities such as munitions testing preclude habitat surveys. Six of the nine accessible sites 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 sites across the entire accessible area of the base for new butterfly occurrences.

To create a spatial data layer for butterfly presence, I first compiled all known sites 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 (http://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

Seven summer (May) and seven winter (December-January) approximately anniversary-dated Landsat-5 Thematic Mapper (TM) images taken from 1985 to 2007 (Table 2.1) were rectified to a mosaic of 1-meter resolution orthorectified digital aerial photographs. Geometric root mean-squared error of independent test points ranged from 15.4 to 28.3 meters. 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: brightness is influenced by soil reflectance, greenness responds to vegetation cover (Cohen and Goward

2004), and wetness responds to standing water and soil/canopy moisture. These techniques have recently been successfully applied to species distribution models (Ranganathan et al. 2007, Zimmermann et al. 2007). Brightness, greenness, and wetness pixels were extracted from wetlands surveyed in 2007. I evaluated relationships between indices by comparing Pearson correlation coefficients across the wetland sample (SAS Institute Inc. 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, Anderson and Martínez-Meyer 2004). Such a prevalence of external factors could lead to indeterminacy and poor resolution of habitat models (Sexton et al. 2006). I 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.— I 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 (Vayssiéres et al. 2000).

I 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 (Ripley 2007, R Development Core Team 2007). To avoid model over-fitting, I pruned the initial tree by setting model complexity to the number of splits at which residual deviance was minimized in cross-validation tests. I then cross-validated the data to assess tree fit and examined both the overall misclassification rate and a confusion matrix of 2007 presences and absences.

Maxent.— I estimated butterfly habitat suitability based on presences observed in 2007 and summer and winter Tasseled Cap brightness, greenness, and wetness from 2007 using Maxent version 3.1 (Phillips et al. 2006). Maxent estimates the realized niche by finding the probability distribution of species presence that is most spread out or 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) 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 (Giovanelli et al. 2008, Ward 2007) and climate change (Hijmans and Graham 2006) on species' distributions.

I 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. I evaluated linear, quadratic, product, threshold, and hinge features.

After fitting the Maxent model, I 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, I mapped the continuous suitability index and also "prime" habitat, identified by thresholding suitability above a certain cutoff value. Maxent calculates and reports several thresholds based on different optimality criteria. Preliminary results showed that interpretation of habitat maps was more practical` by imposing a more stringent threshold on the suitability maps than those provided by Maxent. I 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.

To evaluate the models, I utilized several techniques. First, I used a jackknife test of variable importance to compare models with all combinations of the environmental variables. I 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 (Pearson 2007). 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, I 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-year study period, I 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, I mapped the difference between the 1986 and the 2007 suitability extrapolations. I 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, I 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 greater than 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. I chose the area constraint based on observations of butterfly subpopulations that were unable to persist given smaller patches of habitat (N. Haddad, *pers. communication).*

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

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

in which "PRIME" is prime habitat value, "AREA" is whether the pixel is part of a patch greater than 0.2 ha in size, "INC" is increase in habitat suitability between 1986 and 2007, "¬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, I used fuzzy logic (Zadeh 1965, Roberts 1989), 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 4,337.22 ha, or 6.94% of Ft. Bragg (Figure 3.1). 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. *N. m. 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 (Figure 3.2), 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.

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 (Figure 3.3). 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), 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 (Figure 3.4). Both training and test AUC values were better than random, 0.898 for the training sample and 0.876 for the test sample

(Figure 3.5), suggesting little model over-fitting. Based on the equal training sensitivity and specificity threshold (0.356, see Appendix C for all threshold values), 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 (Table 3.2).

Habitat suitability corresponded to the stream network and riparian zones of the study area (Figure 3.6). Prime habitat patches were located in wetlands on stream channels in small, frequently isolated patches (Figure 3.6). The area covered by prime habitat doubled from 1986 – 2007 (Figure 3.7), ranging from 718.02 ha in 1989 to 1,534.41 ha in 2007. In contrast, predicted suitability-weighted area increased sigmoidally over the study period, rising slowly from a minimum of 6,133.01 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 (Figure 3.8). 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 (Figure 3.7).

N. m. 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 (Figure 3.9). Reintroduction potential is variable within these patches (Figure 3.9, *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.

Discussion

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). 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 sites that are hard to access in the field (Engler et al. 2004). By isolating the niche relationships in occurrence data, presence-only habitat models contribute to conservation by supplying knowledge of species' environmental and spatial distributions (Ferrier 2002, Elith et al. 2006) with less dependence on spatial and observational factors. Using a case study of the endangered Saint Francis satyr butterfly, *N. m. francisci*, I demonstrate 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 (Anderson and Martinez-Meyer 2004, Bourg et al. 2005, 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 species occupies habitat within inaccessible areas of military activity. Opportunities to investigate these sites are extremely rare, but predictive habitat maps can increase search efficiency when opportunities for site surveys are granted. 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 recovery efforts.

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). My results further show how 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 spatiotemporal 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, Cabeza et al. 2004).

My findings confirm that presence-only habitat models can be used to monitor landscape dynamics over time. Given the successional nature of this system, one would expect the possibility of very many changes in habitat suitability over time. Suitability may increase as I detected with increasing numbers of beavers or connectivity through roads. To manage species effectively, long-term species data must be matched by long-term data relating to environmental changes (Early et al. 2008). 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 (Bourg et al. 2005, Early et al. 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

Over time, monitoring and modeling comprise a feedback system (Urban et al. 2002), adapting in recursion toward the goal of precisely locating sites for management action. Guided by versions of the habitat map 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 expertise to refine the model. The model presented here initiates the loop by providing a spatially explicit hypothesis to be tested by further field validation and eventual *N. m. francisci* reintroduction (sensu Sexton et al. 2006).

Predicted suitable *N. m. francisci* habitat is currently distributed across the study area, but most of this habitat is under-occupied by the species. Furthermore, the most suitable *N. m. francisci* habitat is largely unoccupied. The absence of *N. m. francisci* in locations identified as prime habitat may be explained by either of two 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 (Ch.1, Kuefler et al. 2008), a long-recognized limitation of niche-based models (Green 1971). 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. Alternatively, 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 (Ch. 1). The Maxent model identified two areas with high reintroduction potential (Figure 3.9). Because these techniques are improving, we recognize the limitations of using initial models as management guidelines. To adjust for evolving models, I would suggest the

potential of these sites could be increased with additional restoration before reintroduction efforts occur. Restoration through flooding, mimicking beaver activities may further increase the habitat quality of these predicted areas and contribute to successful reintroductions.

A great contribution of predictive habitat maps to rare and endangered species management has been their ability to guide reintroduction and restoration efforts (Pearce and Lindenmayer 1998, Sexton et al. 2006). *N. m. 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 I observe in my 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.

Applications of species distribution models to conserve rare species are numerous. I present a case study using *N. m. francisci*, a species restricted to 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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Table 3.1. Landsat-5 Thematic Mapper imagery time series.

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

Table 3.2. Confusion matrix from cross-validation analysis comparing Maxent model extrapolations with observed *N. m. francisci* presences and absences for 1993, 1997, and 2007.

Year		Absence	Presence	Sensitivity	Specificity	Misclassification Rate
1993 (N = 9)	Absence	NA	1	0.89	NA	11.1%
	Presence	NA	8			
1997 (N = 5)	Absence	0	0	1.0	0.0	60%
	Presence	3	2			
2007 (N = 28)	Absence	16	1	0.9	0.89	10.7%
	Presence	2	9			

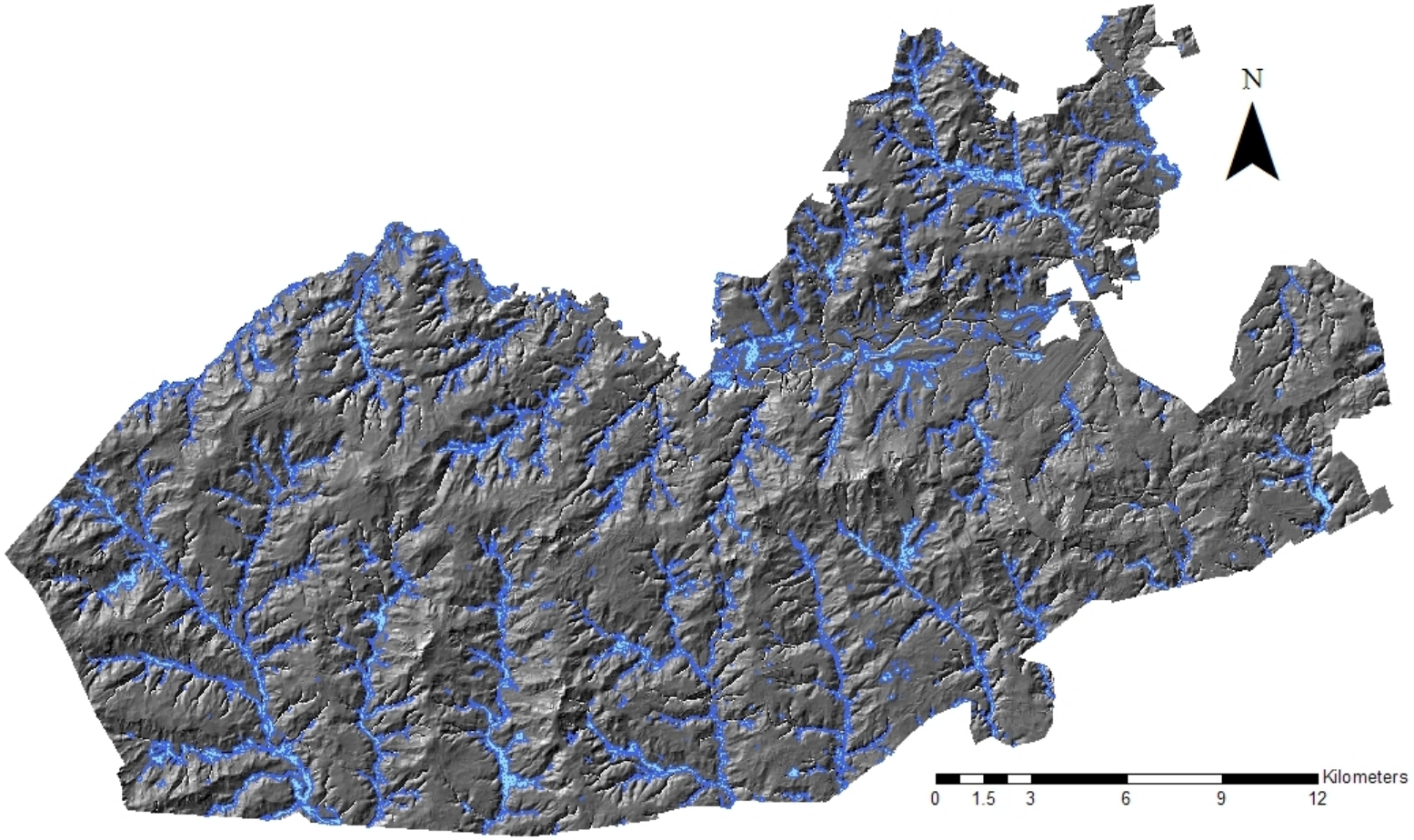


Figure 3.1. Map of National Wetlands Inventory (NWI) delineated wetlands in study area.

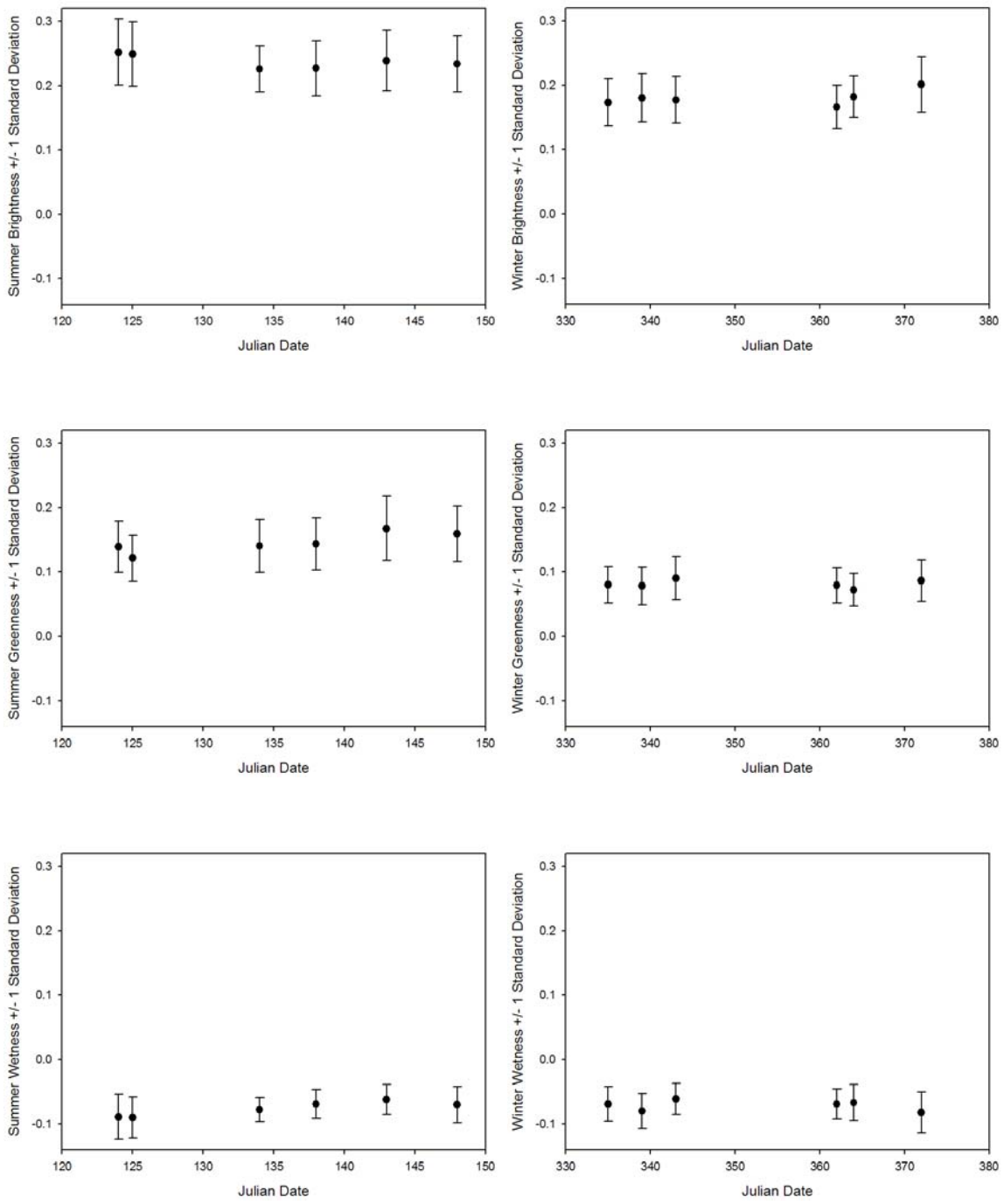
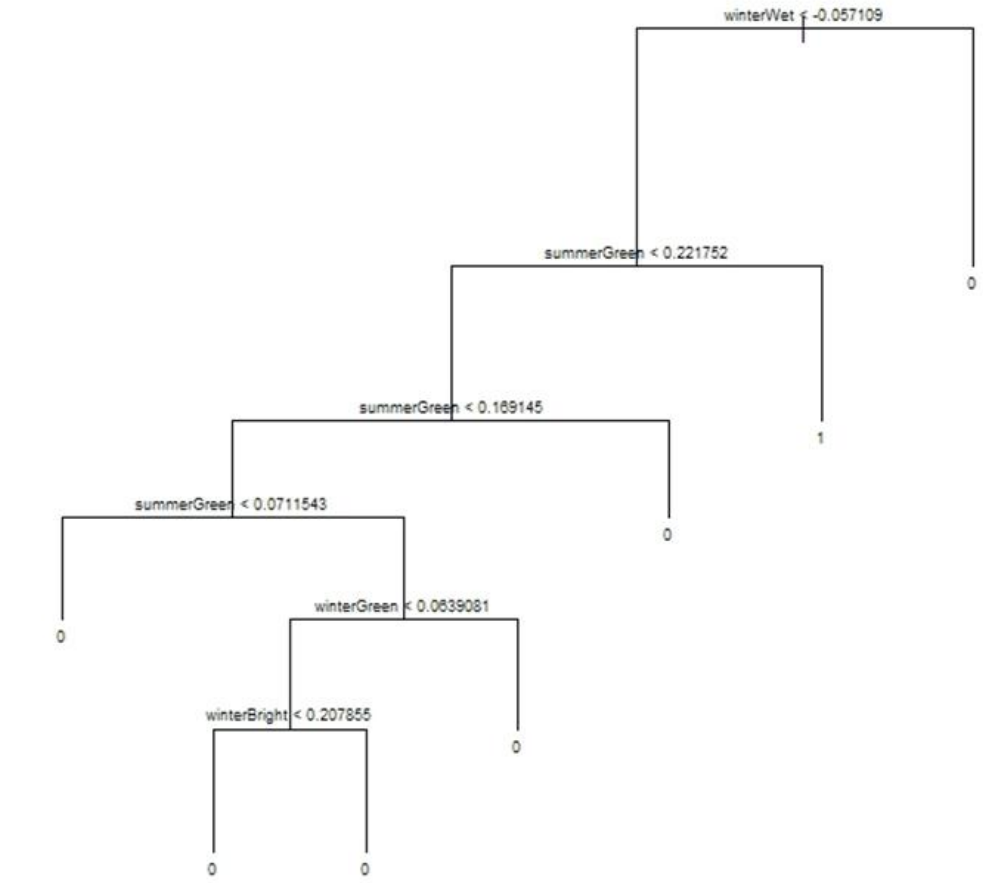
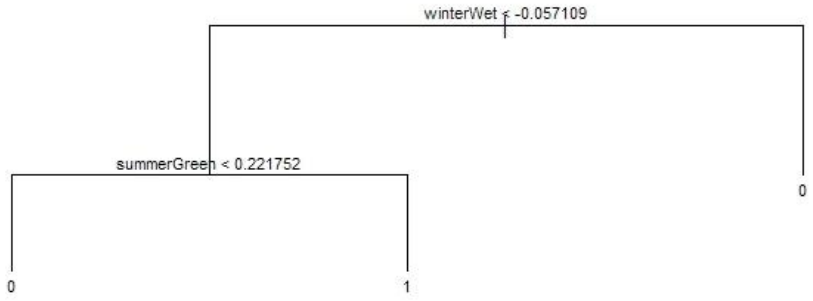


Figure 3.2. Phenological trends in Tassel-Capped environmental indices from seven summer (May) and seven winter (December-January) Landsat-5 Thematic Mapper images taken from 1985 to 2007.Bands 1, 2, and 3 correspond to Tasseled-Cap “brightness”, “greenness”, and “wetness” indices respectively.



a) Whole tree model



b) Pruned tree model

Figure 3.3. Classification and regression trees for a) whole tree and b) pruned tree models where *N. m. francisci* presence/absence is determined by summer and winter Tasseled Cap brightness, greenness, and wetness. The initial tree was pruned by setting model complexity to the number of splits at which residual deviance was minimized in cross-validation tests.

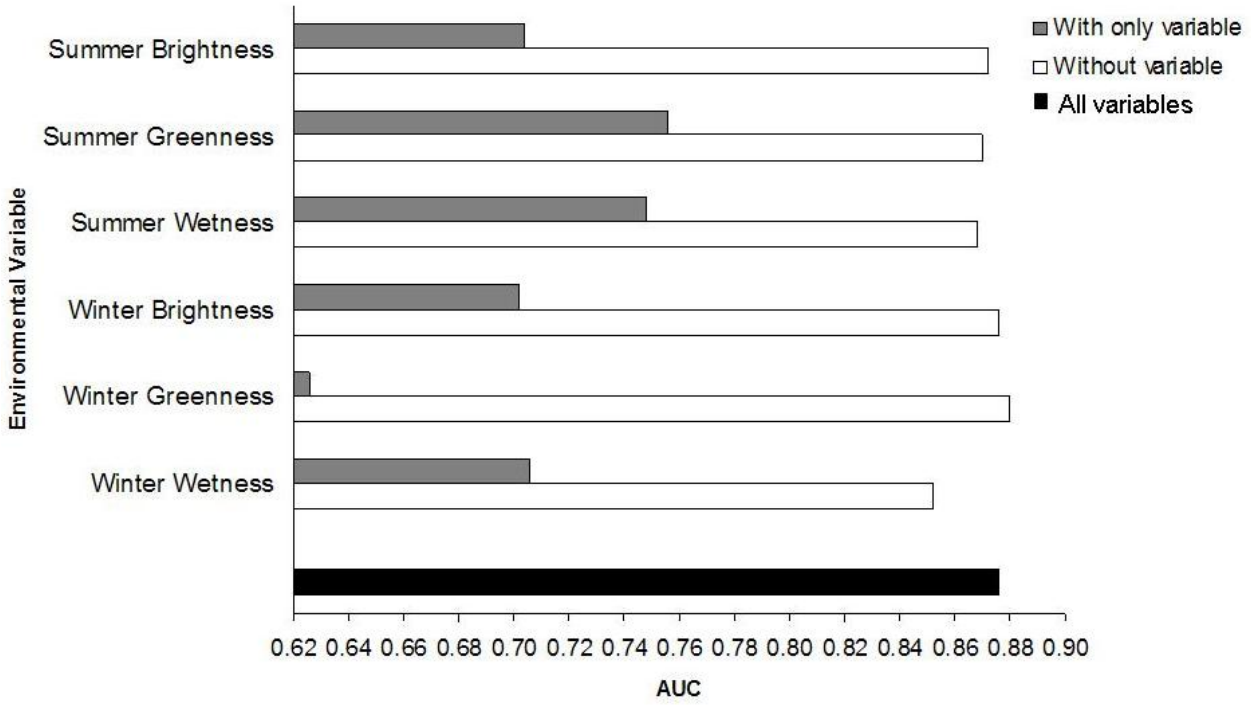


Figure 3.4. Maxent jackknife test of variable importance for test sample comparing all variables including summer and winter Tasseled Cap brightness, greenness, and wetness.

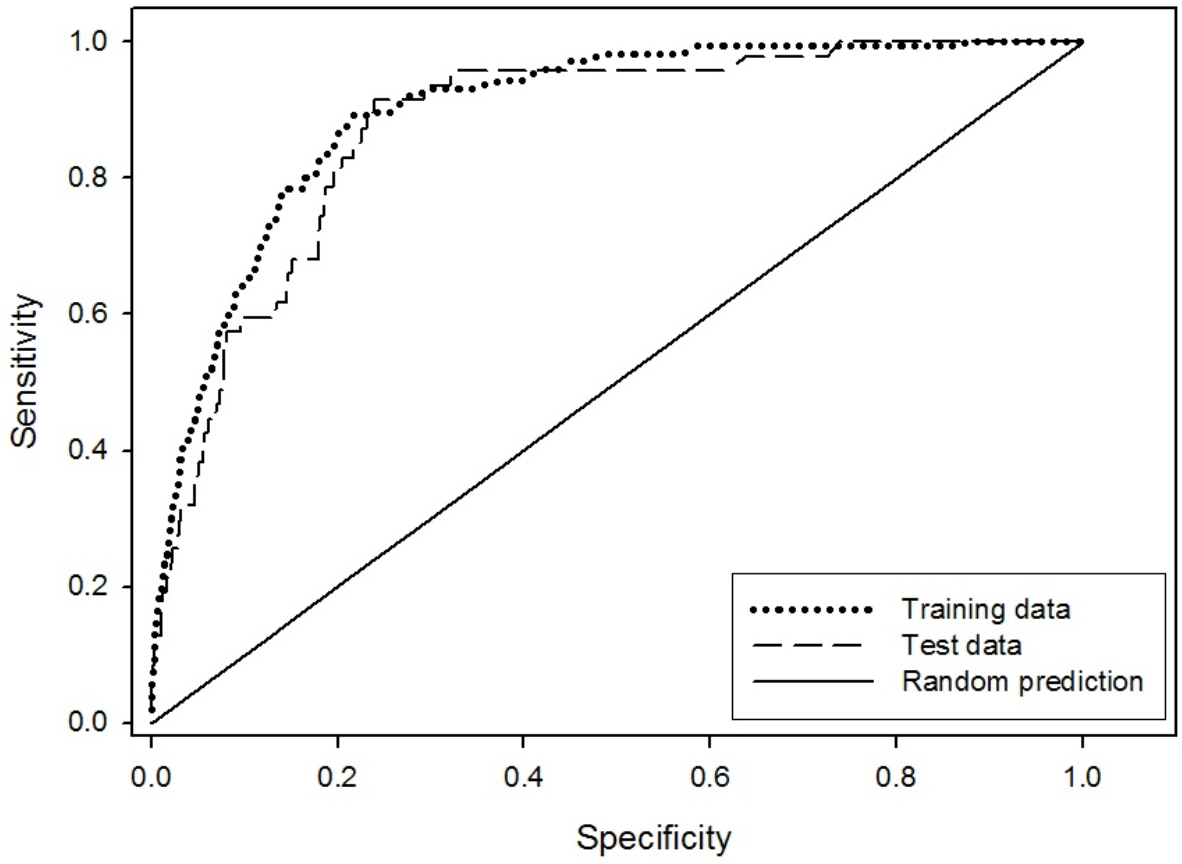


Figure 3.5. Maxent receiver operating characteristic (ROC) curve and calculated the area under the curve (AUC) for training data (n = 176 presence points for 2007) and test data (N = 47 presence points for 2007) as compared to random predictions. Maxent uses an adapted ROC curve that is defined by plotting model sensitivity (1 – omission rate) over specificity (1 – Fractional Predicted Area) across the [0, 1] range of possible thresholds.

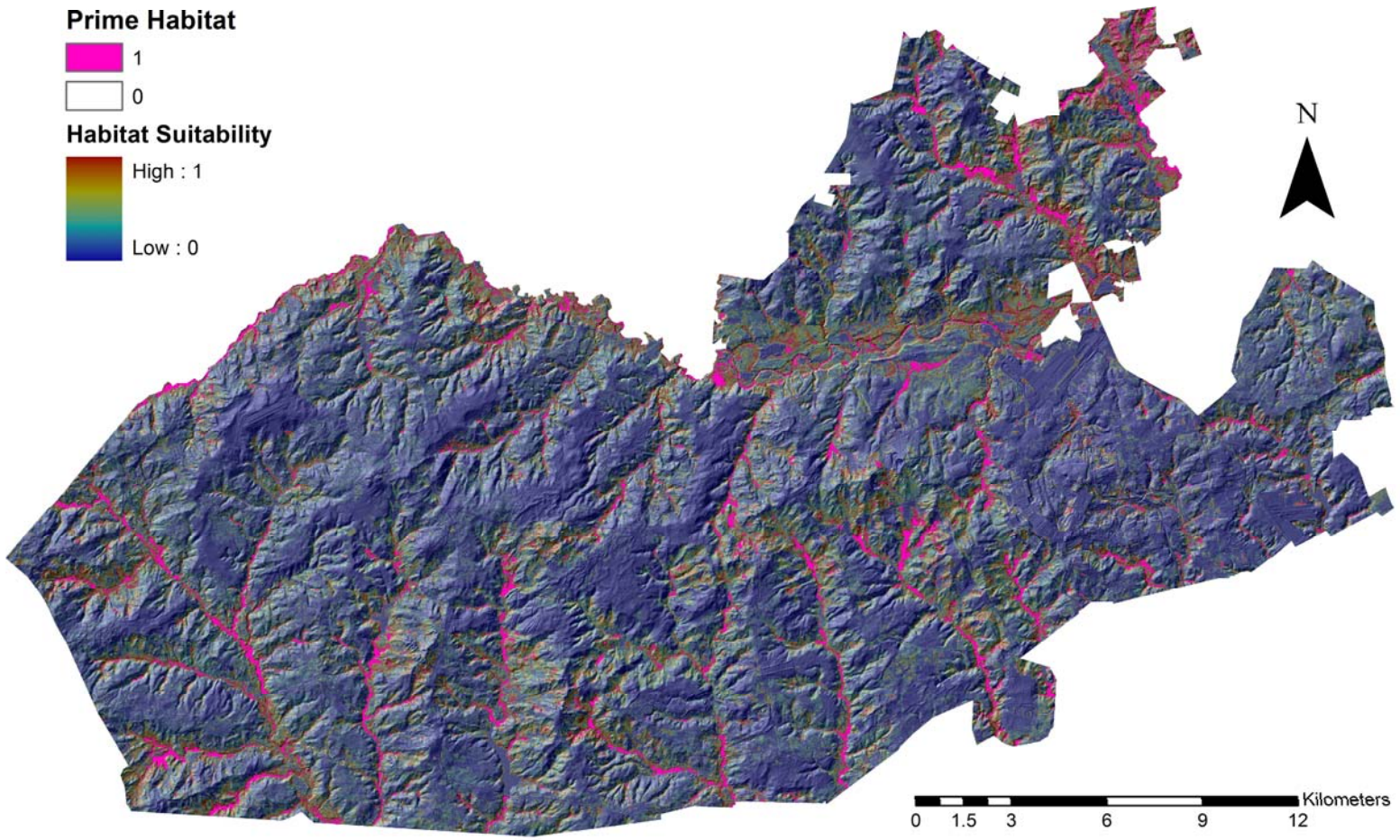


Figure 3.6. Map of total predicted potential habitat suitability and prime habitat areas by Maxent in 2007.

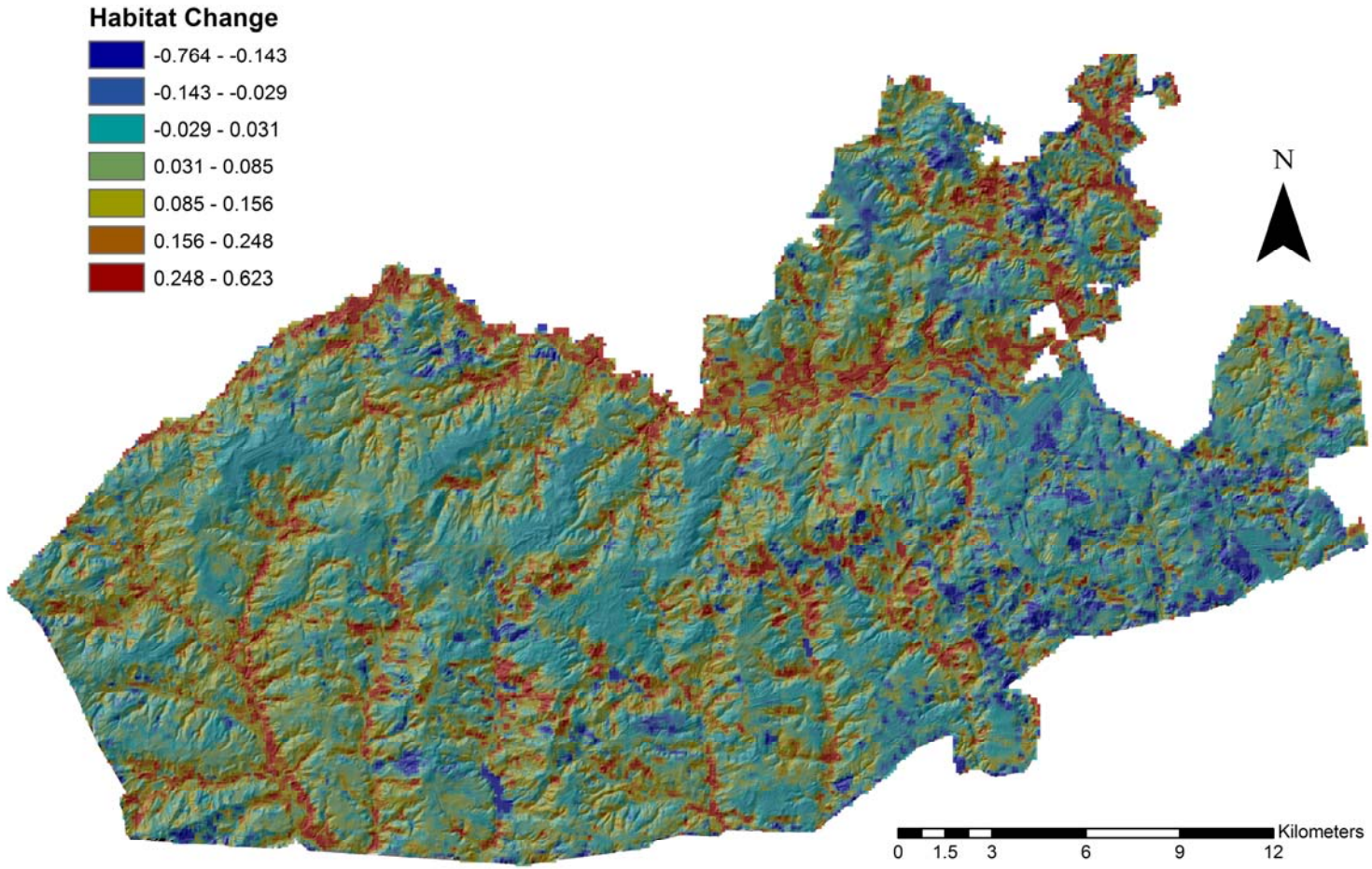


Figure 3.7. Map of predicted changes in habitat suitability by Maxent for the study area 1986-2007.

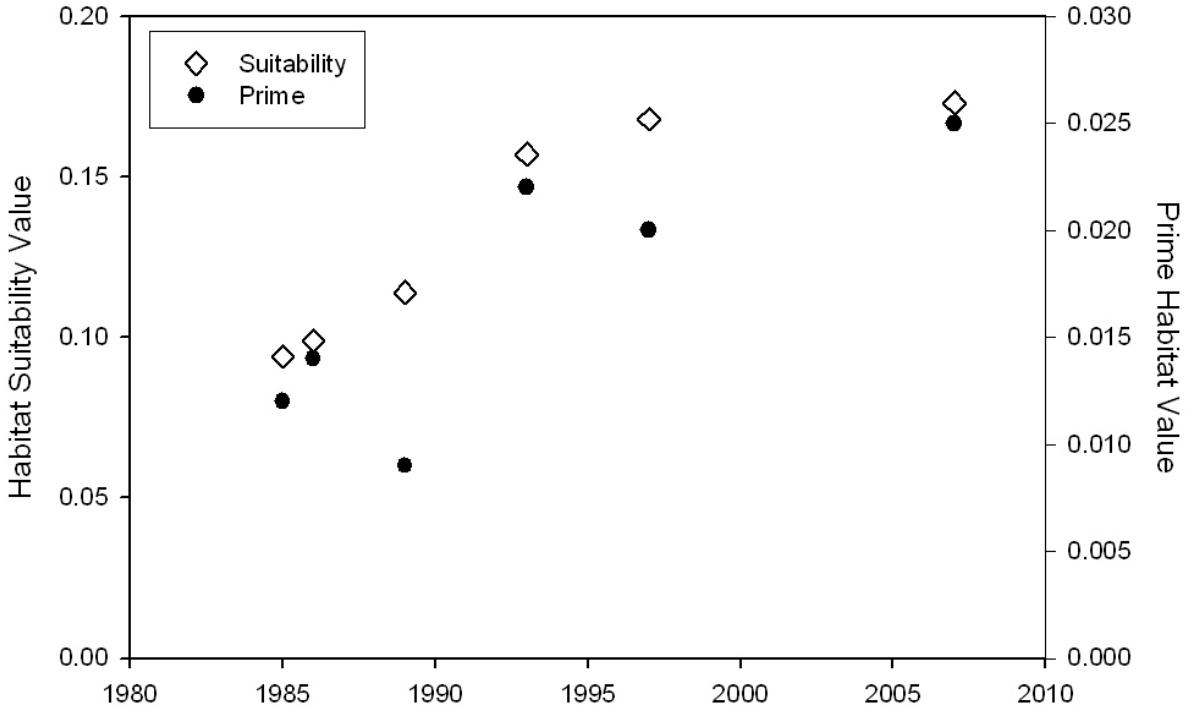


Figure 3.8. Changes in area-weighted logistic habitat suitability indices and prime habitat areas for the study area 1985-2007

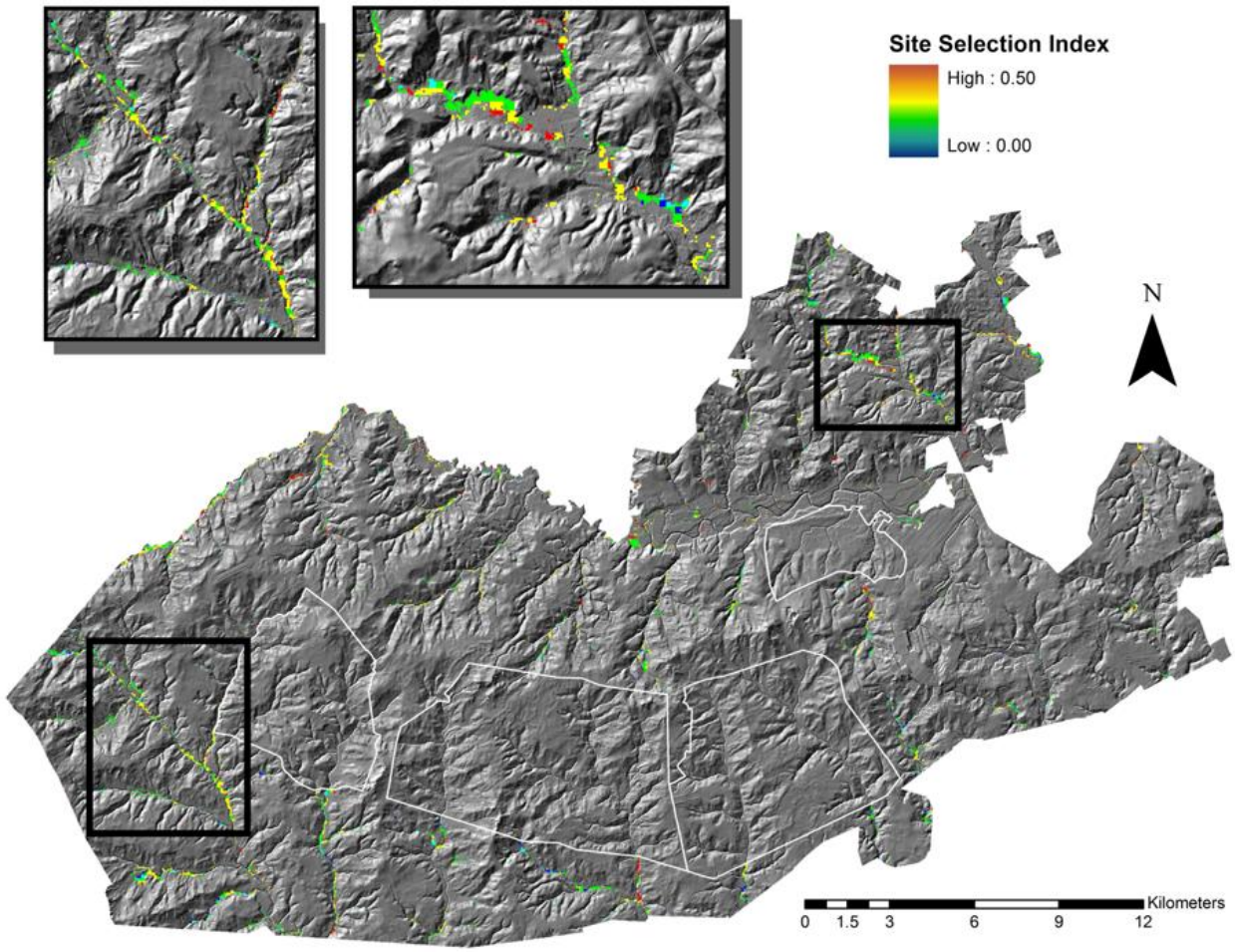


Figure 3.9. Map of predicted priority areas for reintroduction efforts for *N. m. francisci*. Areas outlined in white represent the restricted military areas.

APPENDICES

Appendix A. Plant species found in 2005-2006 plots. Shown here are the family, genus, and specific epithet, life cycle (A = annual, B = biennial, P = perennial), and habit (F = forb, G = graminoid, R = fern, S= shrub, T = tree, V = vine. Life history information was found by using a United States Department of Agriculture Natural Resources Conservation Service Plants Database). All plants were identified using the nomenclature of Radford et al. (1964) except the genera *Dichanthelium* which follow the updated nomenclature of Weakley (2005).

Family	Genus	Species	Life Cycle	Habit
Aceraceae	*Acer*	*barbatum*	P	T
Aceraceae	*Acer*	*rubrum*	P	T
Alismataceae	*Sagittaria*	*longiloba*	P	F
Anacardiaceae	*Rhus*	*copallinum*	P	S/T
Anacardiaceae	*Rhus*	*glabra*	P	S/T
Anacardiaceae	*Toxicodendron*	*radicans*	P	F
Anacardiaceae	*Toxicodendron*	*vernix*	P	T
Apiaceae	*Centella*	*erecta*	P	F
Aquifoliaceae	*Ilex*	*ambigua*	P	S/T
Aquifoliaceae	*Ilex*	*coriacea*	P	S/T
Aquifoliaceae	*Ilex*	*glabra*	P	S
Aquifoliaceae	*Ilex*	*opaca*	P	S/T
Araceae	*Orontium*	*aquaticum*	P	F
Araceae	*Peltandra*	*virginica*	P	F
Asteraceae	*Achillea*	unknown	P	F
Asteraceae	*Ambrosia*	*artemisiifolia*	P	F
Asteraceae	*Bidens*	*cernua*	A	F
Asteraceae	*Cirsium*	*repandum*	P	F
Asteraceae	*Eupatorium*	*album*	P	F
Asteraceae	*Eupatorium*	*capillifolium*	P	F
Asteraceae	*Eupatorium*	*rotundifolium*	P	F
Asteraceae	*Eupatorium*	*serotinum*	P	F
Asteraceae	*Euthamia*	*caroliniana*	P	F
Asteraceae	*Liatris*	*cokeri*	P	F
Asteraceae	*Pseudognaphalium*	*obtusifolium*	AB	F
Asteraceae	*Senecio*	*vulgaris*	AB	F
Asteraceae	*Solidago*	*latissimifolia*	P	F
Asteraceae	*Taraxacum*	*officinale*	P	F
Betulaceae	*Alnus*	*serrulata*	P	T
Betulaceae	*Carpinus*	*caroliniana*	P	T
Blechnaceae	*Woodwardia*	*areolata*	P	R
Cabombaceae	*Brasenia*	*schreberi*	P	F
Campanulaceae	*Lobelia*	*elongata*	P	F
Campanulaceae	*Lobelia*	*glandulosa*	P	F
Campanulaceae	*Lobelia*	*nuttallii*	P	F
Caprifoliaceae	*Viburnum*	*nudum*	P	S/T
Caprifoliaceae	*Viburnum*	*nudum var. cassanoides*	P	S/T
Clethraceae	*Clethra*	*alnifolia*	P	S
Clusiaceae	*Triadenum*	*tubulosum*	P	F
Convolvulaceae	*Ipomoea*	*pandurata*	P	F/V
Cornaceae	*Cornus*	*florida*	P	S/T
Crassulaceae	*Penthorum*	*sedoides*	P	F
Cupressaceae	*Chamaecyparis*	*thyoides*	P	T
Cuscutaceae	*Cuscuta*	unknown	P	V
Cyperaceae	*Carex*	*albolutescens*	P	G

Cyperaceae	*Carex*	*atlantica*	P	G
Cyperaceae	*Carex*	*collinsii*	P	G
Cyperaceae	*Carex*	*mitchelliana*	P	G
Cyperaceae	*Carex*	*debilis*	P	G
Cyperaceae	*Carex*	*glaucescens*	P	G
Cyperaceae	*Carex*	*grayi*	P	G
Cyperaceae	*Carex*	*lonchocarpa*	P	G
Cyperaceae	*Carex*	*lurida*	P	G
Cyperaceae	*Carex*	*muehlenbergii*	P	G
Cyperaceae	*Carex*	unknown	P	G
Cyperaceae	*Carex*	*stricta*	P	G
Cyperaceae	*Carex*	*turgescens*	P	G
Cyperaceae	*Dulichium*	*arundinaceum*	P	G
Cyperaceae	*Eleocharis*	*quadrangulata*	P	G
Cyperaceae	*Eleocharis*	*tenuis*	P	G
Cyperaceae	*Eleocharis*	*tuberculosa*	P	G
Cyperaceae	*Fuirena*	*squarrosa*	P	G
Cyperaceae	*Rhynchospora*	*chalarocephala*	P	G
Cyperaceae	*Rhynchospora*	*inexpansa*	P	G
Cyperaceae	*Schoenoplectus*	*pungens*	P	G
Cyperaceae	*Scirpus*	*cyperinus*	P	G
Cyrillaceae	*Cyrilla*	*racemiflora*	P	T
Droseraceae	*Drosera*	*capillaris*	AP	F
Dryopteridaceae	*Athyrium*	*filix-femina*	P	R
Ericaceae	*Chamaedaphne*	*calyculata*	P	S
Ericaceae	*Gaylussacia*	*frondosa*	P	S
Ericaceae	*Lyonia*	*lucida*	P	S
Ericaceae	*Lyonia*	*mariana*	P	S
Ericaceae	*Oxydendrum*	*arboreum*	P	T
Ericaceae	*Vaccinium*	*arboreum*	P	S
Ericaceae	*Vaccinium*	*corymbosum*	P	S
Ericaceae	*Vaccinium*	*crassifolium*	P	S
Ericaceae	*Vaccinium*	*tenellum*	P	S
Ericaceae	*Vaccinum*	unknown	P	S
Eriocaulaceae	*Syngonanthus*	*flavidulus*	P	F
Fabaceae	*Apios*	*americana*	P	V
Fabaceae	*Gleditsia*	*triacanthos*	P	S/T
Fabaceae	*Kummerowia*	*striata*	A	F
Fabaceae	*Lespedeza*	unknown	P	F
Fabaceae	*Tephrosia*	unknown	P	F
Fabaceae	*Trifolium*	*repens*	P	F
Fabaceae	*Vicia*	*villosa*	P	F
Fabaceae	*Astragalus*	*michauxii*	P	F
Fagaceae	*Quercus*	*laevis*	P	T
Fagaceae	*Quercus*	*laurifolia*	P	T
Fagaceae	*Quercus*	*marilandica*	P	T
Fagaceae	*Quercus*	*nigra*	P	T
Fagaceae	*Quercus*	*palustris*	P	T
Fagaceae	*Quercus*	*phellos*	P	T
Fagaceae	*Quercus*	*stellata*	P	T
Grossulariaceae	*Itea*	*virginica*	P	S
Hamamelidaceae	*Liquidambar*	*styraciflua*	P	T

Hippocastanaceae	*Aesculus*	*glabra*	P	T
Hypericaceae	*Hypericum*	*crux-andreae*	P	F
Hypericaceae	*Hypericum*	*hypericoides*	P	F
Hypericaceae	*Hypericum*	*lloydii*	P	F
Iridaceae	*Iris*	*virginica*	P	F
Iridaceae	*Sisyrinchium*	unknown	P	G
Juglandaceae	*Carya*	*ovata*	P	T
Juncaceae	*Juncus*	*acuminatus*	P	G
Juncaceae	*Juncus*	*canadensis*	P	G
Juncaceae	*Juncus*	*debilis*	AP	G
Juncaceae	*Juncus*	*effusus*	P	G
Juncaceae	*Juncus*	*scirpoides*	P	G
Juncaceae	*Juncus*	unknown	P	G
Juncaceae	*Juncus*	*tenuis*	P	G
Lamiaceae	*Lycopus*	*virginicus*	P	F
Lamiaceae	*Monarda*	*punctata*	ABP	F
Lamiaceae	*Scutellaria*	*elliptica*	P	F
Lamiaceae	*Scutellaria*	*integrifolia*	P	F
Lamiaceae	*Scutellaria*	*nervosa*	P	F
Lauraceae	*Lindera*	*benzoin*	P	S
Lauraceae	*Persea*	*borbonia*	P	S/T
Lauraceae	*Sassafras*	*albidum*	P	S/T
Lentibulariaceae	*Utricularia*	*inflata*	P	F
Liliaceae	*Smilax*	*laurifolia*	P	V
Liliaceae	*Smilax*	*rotundifolia*	P	V
Liliaceae	*Smilax*	*walteri*	P	V
Logainiaceae	*Gelsemium*	*sempervirens*	P	F
Lycopodiaceae	*Lycopodiella*	*alopecuroides*	P	F
Magnoliaceae	*Liriodendron*	*tulipifera*	P	T
Magnoliaceae	*Magnolia*	*acuminata*	P	T
Magnoliaceae	*Magnolia*	*virginiana*	P	T
Melastomataceae	*Rhexia*	*virginica*	P	F
Myricaceae	*Morella*	*caroliniensis*	P	S/T
Myricaceae	*Morella*	*cerifera*	P	S/T
Nymphaeaceae	*Nuphar*	*lutea, spp. sagittifolia*	P	F
Nymphaeaceae	*Nymphaea*	*odorata*	P	F
Osmundaceae	*Osmunda*	*cinnamomea*	P	R
Pinaceae	*Pinus*	*palustris*	P	T
Pinaceae	*Pinus*	*serotina*	P	T
Pinaceae	*Pinus*	unknown	P	T
Poaceae	*Aristida*	*stricta*	P	G
Poaceae	*Arundinaria*	*gigantea*	P	G
Poaceae	*Chasmanthium*	*laxum*	P	G
Poaceae	*Dichanthelium*	*scabriusculum*	P	G
Poaceae	*Dichanthelium*	*scoparium*	P	G
Poaceae	*Glyceria*	*obtusa*	P	G
Poaceae	*Leersia*	*hexandra*	P	G
Poaceae	*Sporobolus*	*vaginiflorus*	A	F
Polygalaceae	*Polygala*	*lutea*	B	F
Polygonaceae	*Polygonum*	*sagittatum*	AP	F
Potamogetonaceae	*Potamogeton*	*confervoides*	P	F
Potamogetonaceae	*Potamogeton*	*diversifolius*	P	F

Pteridaceae	*Pteridium*	*aquilinum*	P	R
Ranunculaceae	*Xanthorhiza*	*simplicissima*	P	F
Rosaceae	*Rubus*	unknown	P	S
Rosaceae	*Sibbaldiopsis*	*tridentata*	P	F
Rosaceae	*Photinia*	*pyrifolia*	P	S
Rubiaceae	*Diodia teres*	*teres*	P	F
Salicaceae	*Salix*	*sericea*	P	F
Sarraceniaceae	*Sarracenia*	*flava*	P	F
Sarraceniaceae	*Sarracenia*	*rubra*	P	F
Scrophulariaceae	*Mimulus*	*ringens*	P	F
Solanaceae	*Solanum*	*carolinense*	P	F
Sparganiaceae	*Sparganium*	*americanum*	P	G
Symplocaceae	*Symplocos*	*tinctoria*	P	S/T
Typhaceae	*Typha*	*latifolia*	P	F
Ulmaceae	*Celtis*	*occidentalis*	P	S/T
Urticaceae	*Pilea*	*pumila*	P	F
Verbenaceae	*Callicarpa*	*americana*	P	S
Violaceae	*Viola*	*sororia*	AP	F
Viscaceae	*Phoradendron*	*leucarpum*	P	S
Vitaceae	*Parthenocissus*	*quinquefolia*	P	V
Vitaceae	*Vitis*	*rotundifolia*	P	V
Vitaceae	*Wisteria*	*frutescens*	P	T
Xyridaceae	*Xyris*	*caroliniana*	P	G
Aceraceae	*Acer*	*barbatum*	P	T

Appendix B. Explanation of variables calculated in model simulations.

Variable name	Variable notation	Estimation
Disturbance rate	d	Varied for each succession model
Succession rate	s	1-d
Proportions of patches in each stage	P_{stage}	N_i/N_{total}
Total # of patches in the landscape	N_{total}	Sum of all stages in stage vector, r
# of disturbed patches in each stage	$N_{disturb}$	$N_i * d$ for each stage
# of patches that succeed to next stage in each stage	$N_{succeed}$	$N_i * s$ for each stage
# of patches that remain in a stage type after disturbance and succession	N_{remain}	
# of patches that are available for occupation given the occupancy rule in each stage	$N_{occrule}$	
Occupancy rate	b	
# of patches with current occupants in each stage	$O_{current}$	$N_{remain} * P_{remain}$
# of patches with new arrivals in each stage	O_{new}	$N_{occrule} * P_{unocc} * b$
Total # of occupied patches in each stage	O_{total}	$O_{current} + O_{new}$
Proportion of occupied patches	P_{occ}	$O_{total} / N_{occrule}$
Proportion of unoccupied patches	P_{unocc}	1- P_{occ}
Proportion of patches that remain in a stage type after disturbance and succession	P_{remain}	
Total proportion of landscape occupied	P_{total}	O_{total} / N_{total}

Appendix C. Maxent thresholds and corresponding omission rates. When test data are available, binomial probabilities are calculated exactly if the number of test samples is at most 25, otherwise using a normal approximation to the binomial. These are 1-sided p-values for the null hypothesis that test points are predicted no better than by a random prediction with the same fractional predicted area (Phillips et al. 2006).

Logistic Threshold	Description	Fractional predicted area	Training omission rate	Test omission rate	P-value
0.035	Fixed cumulative value	0.680	0.006	0.021	<0.0001
0.094	Fixed cumulative value	0.465	0.028	0.043	<0.0001
0.164	Fixed cumulative value	0.344	0.068	0.043	<0.0001
0.004	Minimum training presence	0.871	0.000	0.000	0.004
0.251	10^{th} percentile training presence	0.259	0.097	0.085	<0.0001
0.356	Equal training sensitivity and specificity	0.179	0.182	0.319	<0.0001
0.307	Maximum training sensitivity plus specificity	0.216	0.216	0.170	<0.0001
0.334	Equal test sensitivity and specificity	0.196	0.196	0.191	<0.0001
0.275	Maximum test sensitivity plus specificity	0.240	0.240	0.085	<0.0001
0.057	Blance training, omission, predicted area and threshold value	0.579	0.579	0.043	<0.0001
0.160	Equate entropy of thresholded and non-thresholded distributions	0.349	0.349	0.043	<0.0001