Research

Ecosystem engineers maintain a rare species of butterfly and increase plant diversity

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We evaluated whether ecosystem engineers can accomplish two conservation goals simultaneously: (1) indirectly maintain populations of an endangered animal through habitat modification and (2) increase riparian plant diversity. We tested for effects of a prominent ecosystem engineer, the beaver *Castor canadensis*, on populations of St. Francis' satyr butterfly *Neonympha mitchellii francisci* and plant species richness and composition. We performed our test by surveying riparian vegetation communities in all stages of beaver-influenced wetland succession. We found that beavers created wetland habitats that supported plant species not found elsewhere in riparian zones and increased plant species diversity across the landscape by creating a novel combination of patch types. Our results confirmed what others have found about engineering effects on plant diversity, but these results further demonstrated a case where ecosystem engineers indirectly maintain populations of rare animals by modifying the composition and diversity of plant communities within wetlands. Our research demonstrates how an ecosystem engineer can influence habitat availability and composition of plant communities important for an endangered insect, and maintain overall plant species diversity by increasing habitat heterogeneity.

Many populations of critically rare and endangered species have habitat requirements of specific successional stages (Thomas 1994, Walters et al. 2002, Thomas and Hanski 2004). For these species, succession can provide new habitats for colonization (Pendergrass et al. 1999, Braun et al. 2001), but can also increase extinction risk as vegetation that rare animals use as food or shelter is lost. Successional dynamics may, in turn, be altered by organisms that create conditions necessary for critical food resources (e.g. host plants), or diverse habitat structure that rare animals may require (e.g. nesting trees) that may otherwise be unavailable with continued vegetative succession and no disturbance. These ecosystem engineers (Jones et al. 1994, 1997) can physically modify the composition and diversity of plant communities (Wright et al. 2002, Anderson et al. 2006, Badano and Cavieres 2006) by creating a variety of habitats at different successional stages across the landscape (Wright et al. 2002, 2003). Given their ability to initiate or alter successional dynamics (McMaster and McMaster 2000, Bruno et al. 2003), ecosystem engineering may play an important role in determining the abundance of rare species that depend on disturbed habitats (Pintor and Soluk 2006) by changing the availability of local resources.

The physical impacts of ecosystem engineers on the environment can be both positive and negative from the perspective of individual species (reviewed by Jones et al. 1997). By creating habitats with unique communities, engineering activities could allow more species to persist across the landscape

(Wright et al. 2002, Wright 2009). However, engineering may also negatively affect ecosystems by reducing species diversity (Anderson and Rosemond 2007) or facilitating species invasions (Crooks 2002, Martínez Pastur et al. 2006, Badano et al. 2007). In cases where engineers may affect plant diversity and rare species, the optimal level of ecosystem engineering necessary to preserve rare species may differ from the level of activity needed to maximize total species diversity. This is because the mechanisms by which ecosystem engineers affect rare species and species richness differ; whereas 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), their effects on rare animals more likely depends on specific plant species used for food or shelter. As a result, balancing these effects of ecosystem engineering may lead to tradeoffs between two conservation goals, of creating favorable conditions for rare species and of increasing overall species diversity.

We evaluated how the activities of beavers *Castor canadensis*, the primary agent of disturbance responsible for the creation and maintenance of wetland habitats at our study site (Bartel 2008), modified habitats through dam creation, flooding, and initiating local vegetative succession, and thus affected 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 less than

20 ha in central North Carolina (Haddad et al. 2008, Kuefler et al. 2008). The butterflies occur in several subpopulations in wetland meadows along streams where their presumed larval host plants *Carex* sp. are found. We hypothesized that beaver, by facilitating vegetative succession, create habitats containing *N. m. francisci* host plants, thereby increasing the presence of *N. m. francisci* populations (Fig. 1). 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.

We examine how ecosystem engineers can influence two conservation goals: creating habitat for a critically rare species and increasing biodiversity. We predicted that beavers as ecosystem engineers 1) increase the densities of plant species that may serve as butterfly host plants and therefore increase wetland occupancy of a rare butterfly, and 2) increase landscape-level plant species diversity. By creating habitat patches with unique conditions, beaver activities may allow species to persist in engineered habitats that otherwise would be not found in the landscape, thus causing higher total plant diversity. In light of these predictions, we return in the discussion to evaluate the tradeoffs that may be caused by engineers between the preservation of a rare species and conservation of species diversity in general.

Methods

Field surveys

We conducted our research on Fort Bragg Military Reservation in south central North Carolina (35°07′30′′N, 79°08′30′′W) located within the Southeastern Mixed Forests ecoregion (Ricketts et al. 1999). To assess beaver effects on butterfly host plant species and plant diversity, we studied wetlands across a successional gradient from open water areas

Figure 1. Conceptual model describing hypothesized links for beaver–butterfly interactions. Photo of *N. m. francisci* by Brian Hudgens.

to riparian forest. We selected sites based on visual analysis of digital aerial photographs available from 1996–2005 (flown at 2-year intervals) and of a beaver impoundment vector layer from 2000 that we updated in 2005 after ground surveys. We selected 48 sites of more than 120 locations with various stages of beaver impact. Sites occurred on four stream drainages (referred to as C, D, E and I). Sites were classified by drainage, size, 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 (see Bartel 2008 for detailed descriptions of wetland types). Through ground surveys on each of the four streams, we selected three replicates of each habitat type. We defined a patch as a single area of one habitat type. Subpopulations of *N. m. francisci* occur on stream drainages D and E. A single remnant subpopulation existed on C, which may have been one individual disperser. Butterflies have never been observed on stream drainage I since surveys began in 1992.

In summer 2005, we surveyed vegetation using 1-m^2 quadrats (n = 614) to determine plant community diversity and composition. Because open water patches tended to be larger in area, we surveyed a maximum of 30 plots adjacent to the pond edge with equal distance between plots (n = 212). In all other habitat types, we located plots along transects 1 m from the stream edge or standing water with 10 m between consecutive plots. We delineated the borders of all sites at topographic breakpoints where the wetland met the upland interface. We 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). All plants were identified using the nomenclatures of Radford et al. (1964) and Weakley (2005). 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.

With data collected in 2005, we performed sample-based rarefaction to calculate species accumulation curves with EstimateS 7.5 (Colwell 2005). We then evaluated whether our samples were effectively capturing most of the species in each patch. Subsequently, to ensure adequate sampling of the plant communities, we expanded plot sizes in a subset of the original plots to 3 × 8 m in 2006 (n = 219). We used the location of the 1m^2 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 patch area. For comparison with the larger plots, we resampled the smaller 1-m^2 plots (n = 219) that occurred within the larger plots for all wetland patches. For most analyses, we used data from the larger 3 × 8 plots from 2006. To evaluate the relationship between butterfly population sizes and host plant abundance, we used vegetation data collected from 1-m^2 plots because we had data from this scale in both 2005 and 2006.
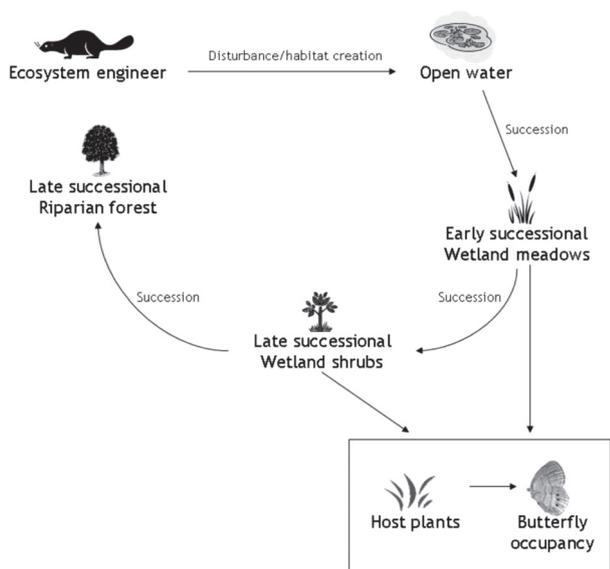
Data analysis

We first assessed how host plant composition influenced butterfly patch occupancy. Subpopulation sizes for *N. m. francisci* were estimated using modified Pollard-Yates transect counts (Pollard 1977) and mark–release–recapture techniques (Kuefler et al. 2008). Second, we examined how ecosystem engineers affected plant abundance and composition in butterfly habitats. Third, we 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. We focused our analysis on the percent cover of six species of *Carex*: *C. atlantica, C. glaucescens, C. lonchocarpa, C. lurida, C. mitchelliana* and *C. stricta.* We also grouped several less common species that occupied patches 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, we used an arcsine transformation on percent cover estimates. To examine the effects of host plants on butterfly demographics, we used linear regressions of percent cover of individual *Carex* species and population estimates of *N. m. francisci* from 2005–2006 (Kuefler et al. 2008). In some cases, a single estimate of butterfly populations was made for two patches. For these sites, we aggregated estimates of percent cover of *Carex* species to match the spatial scale of butterfly population estimates (Kuefler et al. 2008).

To quantify the characteristics of the host plant community that determine butterfly presence, we compared habitat type, stream drainage, and estimates of percent cover for individual *Carex* species, combined Carex species, total graminoids, total shrubs, total woody species (combined shrubs and trees), and total plant species richness 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), we fit a CART to model the probability of butterfly presence.

To assess the effects of ecosystem engineering on plant communities that support *N. m. francisci*, we examined how beaver activities affected different species of *Carex*, the proposed host plants of *N. m. francisci*, at the patch scale utilizing several nonparametric techniques. First, we performed an indicator species analysis using percent cover estimates of the seven *Carex* taxa we studied to test the effects of habitat type on the presence and relative abundance of each taxa (McCune and Mefford 2005). Statistical differences were assessed following 5000 randomizations using a Monte Carlo test of significance. We also used patch averages for the individual plant species to examine how engineering affected percent cover of the various *Carex* species in each habitat type using general linear models (GLMs) and mixed models where the fixed effect was habitat type and the random effect was stream drainage (SAS Institute 2004). Lastly, because habitat structure may also influence butterfly dynamics (Hall 2003), we compared differences in percent cover of all graminoids, all shrubs, and all woody species across habitat types using GLMs. In the 1×1 plots, we also examined vertical structure for all plant species occurring between 50–200 cm of height.

To test whether beavers affect plant species diversity, we compared species richness estimates in the four habitat types at three different scales: plot-level (range = 3–6 plots patch-1), patch-level (n = 48), and landscape-level (n = 4 habitat types). Alpha diversity, or diversity within plots (Whittaker 1960), was calculated as the average species richness across plots (n = 219). We 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. To test for differences in plant diversity across patch types, we calculated Chao 2 estimates for each patch (n = 48 patches). We conducted a second, landscape-scale analysis by aggregating patch types, and calculated Chao 2 values based on incidence of species across patches of the same type (n = 4 habitat types; Colwell 2005). We tested for differences in total percent cover and species diversity between stream drainages and habitat types using GLMs and mixed models (SAS Institute 2004).

To estimate the importance of beaver-modified patches for maintenance of species richness at the landscape scale, we used plant community data to run randomized simulations of landscapes containing different proportions of beaver-modified habitats. For all simulations, plots from different patches within the same habitat type were pooled. We 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, we randomly selected 24 plots collected in forested riparian zones, 14 plots from open habitats, six plots from early habitats, and four plots from late habitats. We 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 plant species present in the landscape.

Results

From 2005–2006, we recorded approximately 181 different species of plants, of which 139 were identified with certainty. Unidentified species (n = 42) were assigned to genus when known or growth form (i.e. unknown shrub), or otherwise were removed prior to analyses. The majority of the plants were herbs (104 species), including 10 species of *Carex.*

Effects of host plant composition on butterfly populations

Neonympha mitchellii francisci population sizes were significantly, positively related to percent cover of *C. mitchelliana* ($r^2 = 0.82$, p = 0.002) and *C. atlantica* ($r^2 = 0.72$, p = 0.016) in 2005–2006. CART models showed that estimates of percent cover of > 0.6% *C. mitchelliana* most effectively predicted butterfly presence. 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, we observed five patches occupied by *N. m. francisci* containing abundances of > 0.6% of *C. mitchelliana* consisting of engineered early and late successional habitats (Fig. 2a). 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 (Fig. 2b). The highest densities of *C. mitchelliana* in stream drainages without *N. m. francisci* present were in two patches of unmodified habitats (Fig. 2b).

Ecosystem engineer effects on butterfly habitats

Two lines of evidence showed that beaver engineering can create habitat which indirectly, positively affects butterfly populations. First, indicator species analysis showed differences in *Carex* community composition between patch types. *Carex 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). Second, using GLMs, we found that *C. atlantica* percent cover was significantly higher in late successional habitats ($F_{3,47} = 3.07$, p = 0.038; Fig. 2). *C. mitchelliana* percent cover was lower in open water habitats and highest in early successional habitats, but these trends were not significant (Fig. 3). When stream drainages were categorized by presence or absence of *N. m. francisci*, we detected significant differences in *C. mitchelliana* percent cover between patch type ($F_{3,23} = 7.65$, p = 0.002), stream drainages ($F_{1,47} = 23.5$, p < 0.001), and an interaction effect ($F_{3,23} = 7.47$, p = 0.002). In stream drainages with *N. m. francisci*, estimates of *C. mitchelliana* percent cover were lowest in open water habitats (not present) and highest in early successional habitats.

Ecosystem engineer effects on plant species diversity

Plant species richness at the plot scale was highest in unmodified habitats (mean = 25), was lowest in open water habitats, and increased slightly with successional stage (range = 14–20, Fig. 4a). Mixed models showed statistically significant differences in species richness among both habitat types at the plot scale ($F_{3,214} = 23.35$, p < 0.001) and among stream drainages ($F_{3,214} = 2.79$, p = 0.04). With further analysis, we determined that these differences at the plot scale were explained by differences in total percent cover ($R^2 = 0.36$, $F_{1,219} = 123.86$, p < 0.001). At the patch scale, we found statistically significant differences in estimated
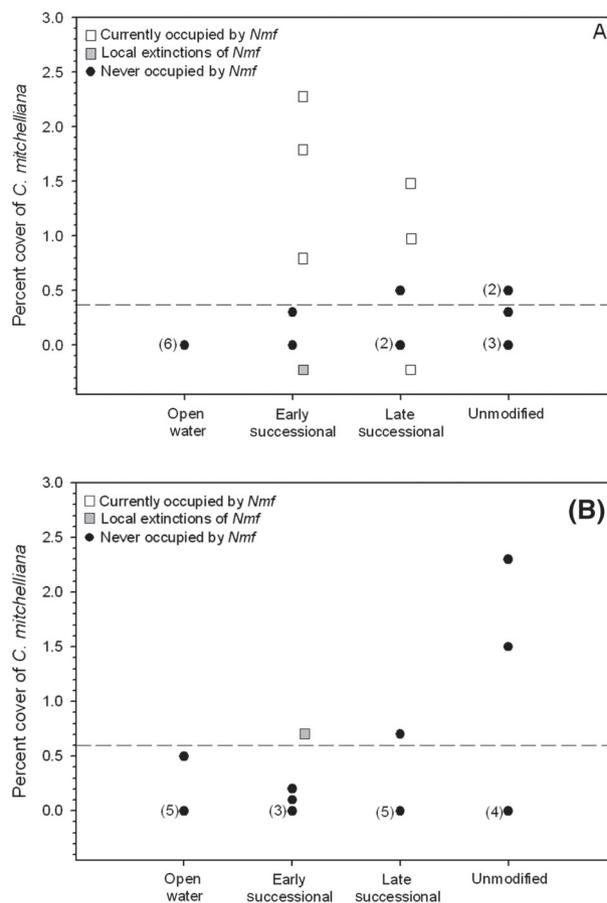

Figure 2. Percent cover of *C. mitchelliana* across habitat types (n = 12 in each habitat) in stream drainages (a) with current *N. m. francisci* (*Nmf*) subpopulations and (b) without current *N. m. francisci* subpopulations. Horizontal line indicates values of percent cover ≥ 0.6%. Open symbols indicate sites currently occupied by *N. m. francisci*. Gray symbols correspond to transitory sites or locations where *N. m. francisci* populations went extinct. Black symbols represent sites that have never been occupied by *N. m. francisci*.

species diversity among patch types but not drainages ($F_{3,41} = 4.28$, p = 0.01), with the biggest difference in species diversity between open water and early successional habitats (Fig. 4b). We also found significant differences in total percent cover of species ($F_{3,47} = 6.99$, p = 0.001) and woody species ($F_{3,47} = 8.20$, p < 0.001) between habitat types, where average percent cover was highest for both groups in unmodified habitats (Fig. 3). We did not detect significant differences in total percent cover of graminoids between habitat types (Fig. 3).

Randomizations showed that estimated species richness was higher in beaver engineered than in unmodified habitats (Fig. 5a). The results of randomly sampling from all four habitat types on the landscape did not differ from those of sampling solely from engineered habitats (Fig. 5a). This is supported by our 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). We found the maximum
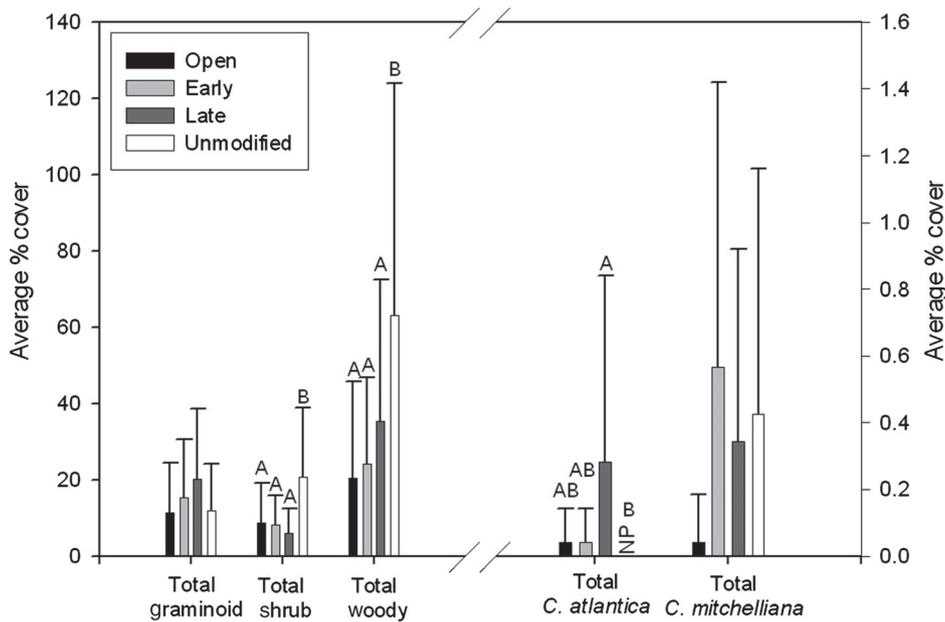
Figure 3. Percent cover of *C. atlantica, C. mitchelliana,* total graminoids, total shrubs, and total woody species across habitat types. NP denotes incidences of plants never present in a given patch type. Error bars represent ± 1 SD. Different letters denote significant differences (p ≤ 0.05) between groups.

species richness occurred with a 30:70 ratio of unmodified and engineered habitats (Fig. 5b), in which case beaver engineering increased landscape-level species diversity by 15% over a landscape with no patches modified by beaver.

Discussion

Our results confirmed findings from other studies that reported ecosystem engineers increased plant diversity, but we go further by showing that they also can indirectly maintain critically rare animals associated with these ecosystems. By resetting vegetative succession, ecosystem engineers facilitated conditions needed by host plant communities that serve as resources for animals. Locally, beavers created wetland habitats that supported plant species not found elsewhere in riparian zones. Ecosystem engineering also increased plant species diversity by creating a combination of patch types across the landscape.

Our findings suggest that beavers as engineers can positively affect a rare butterfly species at a local spatial scale through the modification of the composition and diversity of plant communities. Although we cannot identify definitively the host plant of *N. m. francisci*, our observations that beavers engineer their habitats do not depend on this knowledge. Under the assumption that the host plants are *Carex* spp. (Kuefler et al. 2008), our results showed that *C. atlantica* and *C. mitchelliana* abundance indeed is strongly correlated with the presence and abundance of butterflies. All current *N. m. francisci* populations occur in engineered early and late successional habitats. We found indirect evidence of how ecosystem engineers can affect the distribution of *N. m. francisci* habitats at the patch scale. Non-parametric techniques demonstrated these two species of *Carex* occur more frequently and abundantly in different types of

engineered habitats (early and late successional sites for *C. mitchelliana* and *C. atlantica*, respectively) created by ecosystem engineering. In addition to presence and abundance of host plants, *N. m. francisci* populations may be responding to changes in habitat structure or composition (Hall 2003). We observed the lowest and highest percent cover of total woody species in open water and unmodified habitat types, respectively, where there are no current *N. m. francisci* populations. These two habitat types also had low percent cover of total graminoids in sites occupied by *N. m. francisci*.

At the landscape scale, ecosystem engineers benefited butterfly populations through changing the distribution of wetland plant habitats by producing new habitat patches. In doing so, they can rapidly change a site from suitable to unsuitable habitat (and vice versa). For example, in a single year between 2005 and 2006, six of 12 early successional patches were recolonized by beavers and flooded. Determining the optimal amount of ecosystem engineering for butterfly habitats requires additional analysis of beaver and butterfly spatial population dynamics.

Our model was not perfect, and there were errors of omission and commission. Although CART models showed that the abundance of *C. mitchelliana* was the strongest indicator of *N. m. francisci* presence, it also misclassified several occupied sites containing no *C. mitchelliana*. These sites were modified by beaver, and suggest that there are habitat characteristics, such as alternative hosts, that are not detected by our model. Alternatively, CART models predicted *N. m. francisci* presence at two sites with high abundances of *C. mitchelliana* in unmodified habitats on stream drainages without known *N. m. francisci* subpopulations. These sites may provide evidence for dispersal limitation caused by landscape barriers or the sedentary habits of this butterfly species. Errors may also have been caused
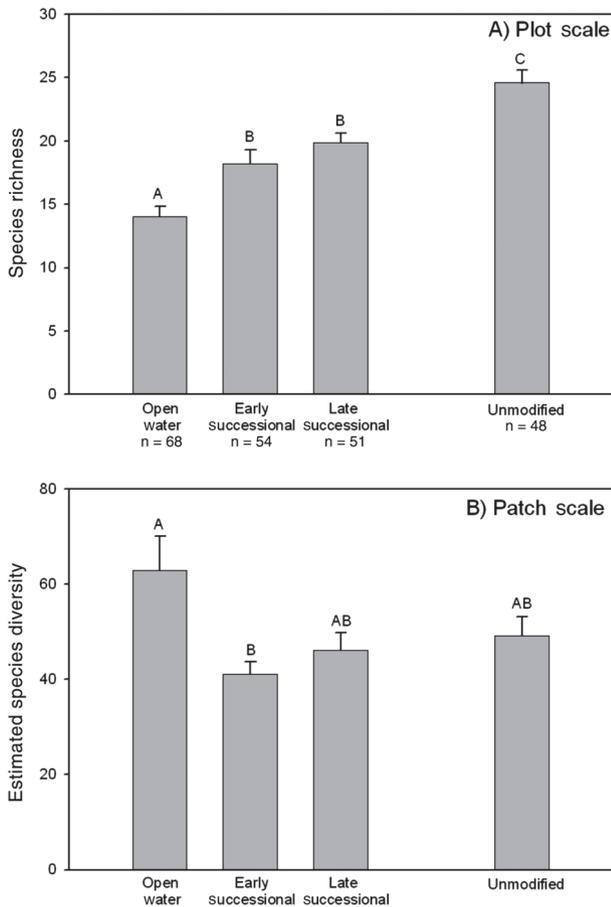
Figure 4. Species richness by habitat type at plot scale (a, n = 219) and patch scale (b, n = 48). Error bars represent +1 SE. Bars with different letters are statistically significantly different at an experimental error rate of p ≤ 0.05 using a Tukey test for multiple comparisons.
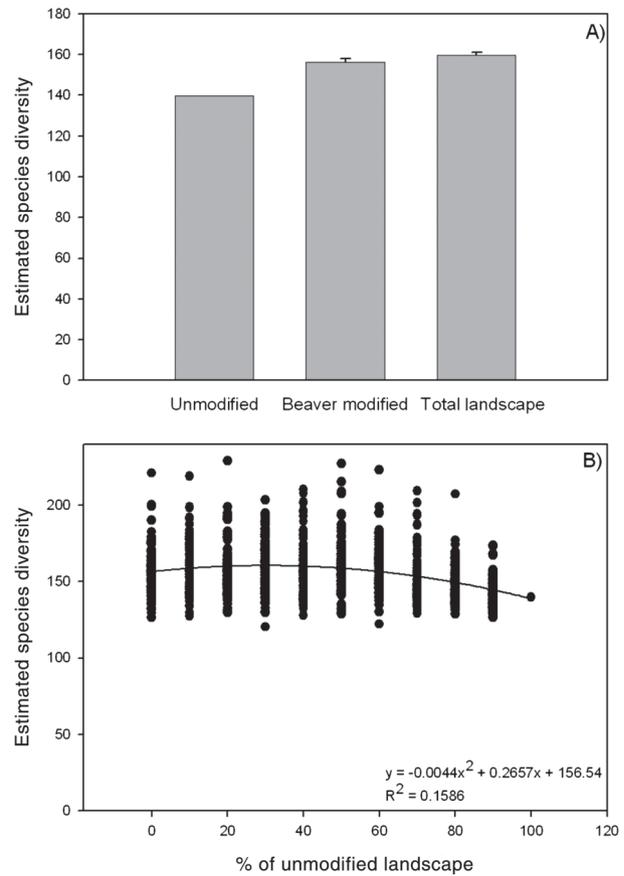

Figure 5. Estimated species diversity of: simulated landscapes composed of unmodified plots, beaver-modified plots, and the total landscape (unmodified + beaver-modified plots) (a), and the relationship between proportion of unmodified habitat in the landscape and estimated species diversity (b). Error bars represent ± 1 SE.

by 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 we utilized consistent criteria in site classification to delineate habitat types, the proximity of these sites may demonstrate the effects of nearby engineering or other types of disturbance.

In addition to impacting the persistence of a rare animal, ecosystem engineering also affected total plant species diversity across spatial scales. At a local scale, engineering resulted in the highest levels of total plant species diversity observed in open water habitats. At the landscape scale, by increasing habitat heterogeneity, beaver activities create wetland habitats capable of supporting herbaceous plant species not found elsewhere in the riparian zone (Wright et al. 2002). Similarly, we found that a mixture of unmodified habitats and engineered habitats at different successional stages is required to maintain a high level of plant species diversity. Landscape simulations suggested that, to maximize plant diversity, ecosystem engineers would affect approximately 70% of habitat area. That said, there is a fairly broad range of habitat modification that will lead to similarly high levels of

richness. Thus, our work shows that engineers can accomplish the dual goals of indirectly maintaining a rare animal and increasing diversity more generally in these riparian ecosystems. Furthermore, given the shape of the relationship between the degree of modification and diversity in this system, managers would have latitude in manipulating the level of disturbance to maximize the success of this rare species while maximizing diversity.

Our study places the strong role of beavers as ecosystem engineers on biodiversity maintenance in a global context (Appendix 1). These results are consistent with others showing that beavers increase local (Wright et al. 2002, Anderson et al. 2006) and landscape-level (Wright et al. 2002) plant diversity, but contrast with studies in South America where beavers are invasive species and had weaker effects at a landscape scale (Anderson et al. 2006, 2009). Whereas native beavers can maintain native biodiversity and the persistence of rare species, invasive beavers can reduce macroinvertebrate diversity (Anderson and Rosemond 2007) and facilitate invasions by plants (Martínez Pastur et al. 2006). Importantly, our work shows how an ecosystem engineer can both increase overall species diversity and positively affect a rare species through habitat.

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 these results are likely to extend to other engineers. Ecosystem engineers can perform many roles and functions; some ecosystem 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. 2009). Ecosystem engineering can facilitate further species invasion (Martínez Pastur et al. 2006, Badano et al. 2007) or aid the persistence of rare species (Pintor and Soluk 2006). Our 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 plant biodiversity. This outcome was facilitated by the creation of a combination of conditions by ecosystem engineers, such that engineered habitats contained species not present in unmodified patches (Jones et al. 1997, Wright et al. 2002). Although we do not know how general this phenomenon is, engineers are most likely to create a win-win situation for both rare species and overall species diversity when: 1) habitat patches that rare species depend on are the same patches that when modified will increase diversity in the landscape, and 2) habitat patches are created at least as quickly as they are destroyed through succession or repeated disturbance. Many animal species have become threatened or endangered as a result of modifications to 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 affected imperiled species and to prevent spread of associated invasive species. Understanding the role of ecosystem engineers in ecosystems can focus conservation, habitat management, and restoration efforts in ecosystems with critically rare species.

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Appendix 1. 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 Martínez Pastur et al. 2006	this study
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
Ecoregion (WWF*)	Eastern Forest/Boreal Transition	Magellanic Subpolar Forests	Southeastern Mixed Forests
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 × 1.0 m²	0.5 m²	1.0 m², 3.0 × 8.0 m²
Beaver history	Native, reintroduced ~ 1910	Exotic, introduced in 1946	Native, reintroduced in 1939
Beaver densities (colonies km-1)	0.5–0.7	0.2–5.8	Unknown
Beaver average occupancy rates, (range)	4.8 years (1–20)	(5–15)	Unknown
Total no. 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 plant species richness?	No	Yes	No
Increased landscape species richness?	Yes	No	Yes

*Ecoregions as defined by World Wildlife Fund