

Habitat restoration alters adult butterfly morphology and potential fecundity through effects on host plant quality

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Abstract. Conservation strategies for threatened species frequently include habitat restoration, but the success of such recovery efforts has been mixed. When the target is an insect herbivore, restoration efforts have traditionally attempted to increase the abundance of its host plant, but these actions' impact on host plant quality has largely been ignored. Here, we test the impact of two forms of habitat restoration, tree removal and stream damming, on the physical and chemical properties of a wetland sedge and on the adult traits of its larval consumer, a wetland butterfly. Tree removal altered plant physical and chemical traits in a manner largely consistent with reduced host plant quality. Females emerging from these plots had fewer mature oocytes in their ovaries upon emergence, suggesting that tree removal has a negative effect on butterfly potential fecundity. Stream damming did not affect plant traits but forewing length increased more steeply with body mass for females from these plots, indicating that small females from dammed plots have a relatively higher wing loading ratio that likely increases the energetic cost of flight. This idea was supported by results from our subsequent capture–mark–recapture study, where both female and male butterflies were less likely to emigrate from dammed plots. Male dispersal was also affected by restoration, but individual body mass rather than wing allometry mediated this effect. Our results highlight the need to consider restoration's impact on host plant quality, in addition to other aspects of habitat quality, when undertaking habitat restoration for threatened herbivores.

Key words: allometry; capture–mark–recapture; habitat quality; potential fecundity; restoration; wetland butterfly.

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INTRODUCTION

Species extinctions are a devastating consequence of the loss of habitat (Haddad et al. 2015). To mitigate the increased extinction risk caused by habitat loss, restoration is often employed to speed the recovery of degraded habitats (Hobbs et al. 2006). For herbivores, restoration strategies typically aim to boost target populations by changing the environment to facilitate the establishment

and growth of their food plants, with the assumption that vulnerable taxa will recover following the restoration of host abundance (the “Field of Dreams” myth sensu Hilderbrand et al. 2005). The effectiveness of such restoration efforts, however, is often unclear (Schultz et al. 2008, Bried et al. 2014), likely in part because these actions ignore restoration's effect on host plant quality (but see Pickens and Root 2008). This is surprising given the well-established relationships between abiotic

conditions (e.g., light, nutrient, and water availability) and plant traits (Tilman and Wedin 1991, Dudley 1996, Poorter 1999) that affect the quality of the plants as food for herbivores (Leather et al. 1998, Awmack and Leather 2002, Klemola et al. 2007). Beyond the indirect effects of restoration mediated through host plant quality, habitat manipulations via restoration can directly affect focal species' habitat quality through changes in the abiotic environment they experience. Here, we test the relationship between larval host plant quality and adult resource allocation to morphology and fecundity. While we investigate plant quality effects in detail, our restoration experiments also account for any direct effects on adult traits.

Restoration often transforms the abiotic environment in ways that can affect not just the abundance of plants but also their quality for herbivores. One commonly employed method to restore open wetland habitat is to remove trees, an action that increases light availability. Increased light availability alters the physical and chemical properties of leaves (Karolewski et al. 2013). Leaves grown in full sun typically have a lower nutritional value, with lower percentage of nitrogen, higher carbon-to-nitrogen ratios, and lower water content, and are tougher than leaves grown in shade (Onoda et al. 2008, Gross et al. 2009, Karolewski et al. 2013). Leaves exposed to higher levels of light may also have higher concentrations of plant defenses (Hemming and Lindroth 1999, Henriksson et al. 2003, Karolewski et al. 2013). For herbivores, these changes often translate into reduced host plant quality because nitrogen is a limiting element that is essential for growth (reviewed by Mattson 1980) and leaf toughness is negatively correlated with herbivory (Coley 1983) and herbivore performance (Feeny 1970). A second form of wetland restoration, stream damming, increases standing water. To increase the rate of CO₂ acquisition, submerged plants often elongate their shoots to keep their leaves above water (Voesenek et al. 2006). Compared to leaves produced by non-submerged plants, these leaves are thin with a high surface area to enhance gas exchange, have a high water content, and have lower secondary plant compounds (Davalos and Blossey 2010). These traits suggest an increase in host plant quality for herbivores.

Changes in plant traits can translate into differences in herbivore fitness. The reduced plant quality of sun leaves resulted in longer caterpillar development times compared to those that fed on shade leaves (Jansen and Stamp 1997, Henriksson et al. 2003). Similarly, leaf beetles fed purple loosestrife (*Lythrum salicaria*) grown in flooded soils had higher survival and oviposited more compared to those fed leaves from well-drained soils (Davalos and Blossey 2010). One possible mechanism behind these fitness differences is that changes in plant quality alter the amount and allocation of nutrients available for reproduction, survival, and dispersal. Butterflies starved for a portion of their last larval instar (thereby limiting larval food quantity) had lower body mass, wing lengths, and wing loading ratios than butterflies fed without restriction (Angelo and Slansky 1984, Boggs and Freeman 2005). The impact of changes in larval food quality, however, is largely unknown (but see Colasurdo et al. 2009). An understanding of the impact of restoration on adult traits mediated through changes in larval food quality is critical to assessing the intended and unintended consequences of restoration for species of conservation concern.

Changes in plant quality caused by restoration may be additionally problematic if they alter traits of threatened species in such a way as to lower their dispersal. Beyond the goal of re-establishing habitat resources, restoration seeks to enhance population viability of focal taxa by maintaining landscape connectivity through dispersal (McAlpine et al. 2016). For butterflies, the ratio of body mass to wing size (i.e., wing loading) is a correlate of dispersal ability (Betts and Wootton 1988), and how wing size scales with body mass is represented by an allometric relationship. Limited food availability can steepen the slope of this relationship (Angelo and Slansky 1984, Boggs and Freeman 2005). While such changes in allometry are often speculated to result in changes in dispersal, joint measurement of allometry and dispersal propensity are rare (but see Berwaerts et al. 2002, Fric and Konvicka 2002). Assessing whether changes in adult morphology translate into ecologically relevant dispersal differences, as we do here, has not previously been performed yet is needed to understand how restoration might alter the dynamics

of patchily distributed species of conservation interest.

We experimentally test the effects of habitat restoration on plant quality and its subsequent effects on adult morphology and reproduction. As a case study, we conducted our tests on the wetland sedge, *Carex mitchelliana*, and the Appalachian brown butterfly, *Satyroides appalachia* Chermock (Lepidoptera: Nymphalidae), whose larvae feed on the sedge. We created experimental restoration plots as a factorial combination of two treatments: tree removal (>90% of the trees removed) and stream damming. We hypothesized that restoration would alter the quality of *C. mitchelliana* leaves, with tree removal decreasing plant quality and stream damming increasing plant quality. We expected that changes in plant quality would manifest in the adult traits of larvae that fed on the plants, with an increased allocation to reproduction in sites with high plant quality and an increased allocation to dispersal in sites with low plant quality.

METHODS

Species and study site

We investigated the effects of wetland restoration on the Appalachian brown, a bivoltine butterfly found in sedge-dominated wetlands at Fort Bragg, North Carolina, USA. While restoration was undertaken to benefit a closely related butterfly, the U.S. federally endangered St. Francis' satyr (*Neonympha mitchellii francisci* Parshall and Kral [Lepidoptera: Nymphalidae]), we could not ethically conduct experiments with St. Francis' satyr on juvenile life stages given its extreme rarity. We expected restoration to enhance Appalachian brown populations in a similar way to St. Francis' satyr because these species share the same landscape, feed on the same plants as larvae, and demonstrate similar dispersal behaviors (Hudgens et al. 2012). Their shared habitats are early-successional wetlands created by abandoned beaver ponds and by fire (Bartel et al. 2010) and are highly ephemeral, with habitat quality quickly degrading as shrubs and hardwoods grow and exclude herbaceous plants, including sedges. Both butterflies exclusively consume sedges in the genus *Carex* as their larval host plants (Kuefler et al. 2008) and do not feed on nectar as adults, dictating that larval

feeding is the only way an individual acquires resources for development and subsequent survival, reproduction, and dispersal. Additionally, females from both species emerge as adults with their full set of oocytes, making the number of oocytes present in their ovaries at the time of emergence a reasonable measure of potential fecundity.

Experimental design

In 2011, we manipulated riparian habitat to mimic primary successional stages of abandoned beaver ponds. Within each of four blocks, we randomly assigned 30 × 30 m plots to one of four habitat restoration treatments: (1) manual removal of 90% of trees ("tree removal"), (2) installation of temporary dams ("damming"), (3) both tree removal and damming, and (4) no manipulation (for details, see Aschehoug et al. 2015). We excluded one of the damming plots from the experiment, making one of the blocks incomplete, because it was colonized by beavers. Tree removal plots succeeded in dramatically increasing the percent cover of *C. mitchelliana*, a host plant for Appalachian brown and St. Francis satyr (Aschehoug et al. 2015).

Plant quality assessment

To capture seasonal variation in plant quality, we sampled *C. mitchelliana* leaves in each restoration plot monthly from April to October 2012, spanning the growing season of *C. mitchelliana*. From each of three *C. mitchelliana* plants in each plot, we randomly harvested five new vegetative ramets (but we did not attempt to collect ramets from the same three plants every month). To minimize moisture loss, samples were sealed in plastic bags, stored in a cooler, and transported back to the laboratory, where they were kept at 4°C overnight prior to the measurement of plant quality traits the following day.

From each plant, we separated five leaves from their stems, blotted them dry to remove any surface water or dirt, weighed them, measured their area using a leaf area meter (CI-202 Portable Laser Leaf Area Meter; CID Bio-Science, Camas, Wisconsin, USA), and dried them at 70°C for 3 d. Following drying, we weighed the leaves again and calculated the specific leaf area as the ratio of leaf area to leaf dry mass. We calculated leaf dry matter content as the ratio of dry mass to fresh

mass. We averaged these two metrics across the five leaves, resulting in a single measurement for each plant.

We measured leaf toughness of three additional fresh leaves from each plant, randomly chosen, using a penetrometer that quantifies the force needed to pierce a hole in a leaf using a 5 mm diameter plunger (Lowman and Box 1983). Because toughness varies by position along the leaf, we took penetrometer measurements at the same distance from the leaf tip for all samples. We punctured each leaf three times and averaged the results across the three leaves.

To assess the nutritional quality of leaves, we ground dried leaves using a Cyclone Sample Mill (UDY, Fort Collins, Colorado, USA) and analyzed samples for percentage of carbon (C), percentage of nitrogen (N), and C:N ratio using a CHN/S Elemental Analyzer (Model 2400 series II; PerkinElmer, Waltham, Massachusetts, USA). We also quantified the percentage of silica (Si) of leaves by first digesting plant tissues using microwave-assisted digestion (Haysom and Ostatek-Boczynski 2006). We then analyzed percentage of Si with an inductively coupled plasma optical emission spectrometer (Model 2000 DV; PerkinElmer; Kraska and Breitenbeck 2010). All labware and chemicals associated with the analysis were prepared in polypropylene or Teflon to eliminate the possibility for Si contamination associated with glass. North Carolina State University's Environmental and Agricultural Testing Service performed all of chemical analyses.

We analyzed plant quality data as a longitudinal study using the function `lmer` in the `lme4` package in R (Bates et al. 2015, R Core Team 2015). Because plots of plant quality traits vs. month showed either no trend or a linear trend over time, we modeled these traits as linear regressions against month (treated as an ordinal variable). In regression analyses, we included as fixed effects the three-way interaction between tree removal, damming, and month, plus all lower-order terms, and we evaluated block and plot as possible random effects, with plant quality traits measured repeatedly for each plot. We began with models that allowed the slope and the intercept of the regression of plant quality traits against month to vary in a correlated fashion among plots, but the slope and intercept

estimates were highly positively correlated among plots for all plant quality traits, indicating both random effects were not needed. As the random variance among blocks did not differ significantly from zero for any plant quality trait, even accounting for the biased *P* values when testing for a nonzero variance (Bates et al. 2015), we eliminated block effect from the models. Next, to compare models lacking random variation in the intercept or slope vs. month to the model that included both (as independent random effects), we tested for random variation among plots in the slope and intercept using likelihood ratio tests. For all plant quality traits, the intercept did not vary independently among plots, but the slope often did. Finally, we refit the resulting models, including among-plot variation in the slope as appropriate, using restricted maximum likelihood. We used the ANOVA function from the `car` package (Fox and Weisberg 2011) in R to perform Wald type II chi-square tests for an influence of the fixed effects (restoration treatments, month, and their interaction) on the plant quality traits. Prior to analysis, C:N ratio and specific leaf area were \ln -transformed and proportion Si was arcsine-square-root-transformed to meet assumptions of normality and homogeneity of variance.

Adult traits

We assessed restoration's effects on butterfly morphology and fitness by rearing Appalachian brown larvae on *C. mitchelliana* plants. Within each of the 15 restoration plots, we installed six cages around *C. mitchelliana* sedges to house developing Appalachian brown larvae (90 cages in total; for details, see Aschehoug et al. 2015). Larvae were the progeny of 68 wild-caught Appalachian brown females from Ft. Bragg wetlands brought into the greenhouse to lay eggs. Appalachian brown larvae from multiple mothers were reared together on potted *C. mitchelliana*, making it impossible to distinguish the parentage of individual larvae. Larvae were reared in the greenhouse until we had enough individuals to populate each cage in an experimental block with five individuals. In practice, this meant that deployed larvae varied in age; of the 450 larvae, 44 (10%) were late first instars, 353 (78%) were second instars, and 53 (12%) were third instars. Larvae were left to develop in cages;

treatment effects on larval survival are reported by Aschehoug et al. (2015).

After larvae pupated, we checked cages daily for the presence of emerged adults. Following Boggs and Freeman (2005), we measured the body mass and forewing length of each individual on the afternoon of eclosion. Sample sizes for males and females, respectively, were 9 and 13 from the tree removal plots, 16 and 15 from the dammed plots, 9 and 10 from the tree removal and dammed plots, and 21 and 16 from the control plots. To evaluate restoration's effects on potential fecundity, we dissected newly emerged, unmated females and counted the number of oocytes in each female's ovaries. The diameter of each oocyte was measured using an ocular micrometer under a dissecting microscope at 4 \times . At this magnification, we classified an oocyte as mature if its diameter was >3.5 ocular micrometer units (0.875 mm; diameters ranged from <0.5 to 6.5 ocular micrometer units). We chose 3.5 ocular micrometer units as the threshold for mature oocytes based on our observation that all oocytes of this size had undergone vitellogenesis (yolk deposition), a precursor to oviposition that is dependent, in part, on larval nutrition (O'Brien et al. 2005).

To test the effects of restoration on the relationship between female potential fecundity, as represented by counts of the total number of oocytes and the number of mature oocytes in a female's ovaries, we used negative binomial generalized linear models with the `glmMADMB` function in the `glmMADMB` package (Fournier et al. 2012, Skaug et al. 2016) in R. The model evaluating restoration's effect on the total number of oocytes included the fixed effects of tree removal, damming, body mass, and their interactions and the nested random effects of cage within plot within block. To determine whether restoration treatment influenced the total number of oocytes when controlling for butterfly mass, we used likelihood ratio tests. For the model evaluating restoration's effect on the number of mature oocytes, we determined that body mass significantly impacted restoration's effect on mature oocyte number (significant interaction between \ln body mass \times damming \times tree removal: $\chi^2_1 = 9.00$, $P = 0.0292$), so we included body mass as an offset in the model. As an offset, we report the effect of restoration at an average body mass. We used

the `glmer.nb` function in the `lme4` package (Bates et al. 2015) and the `effects` function in the `effects` package (Fox 2003) in R to calculate the predicted number of mature oocytes takes into account female body mass.

To assess the effect of restoration on butterfly body mass and forewing length, we used linear mixed models fit by restricted maximum likelihood with the `lmer` function in the `lme4` package (Bates et al. 2015) in R. Body mass was natural log-transformed to meet the assumptions of normality and homogeneity of residual variance. Our initial model contained fixed effects of sex, tree removal, damming, and their interactions, and the random effects of block, plot, and cage, which was nested within plot within block. We examined males and females separately, a division that is biologically reasonable given sexual dimorphism in butterflies. The resulting single-sex models had the fixed effects of tree removal, damming, and their interaction, and the same random effects as the initial model. We used likelihood ratio tests to determine whether the interaction between tree removal and damming was significant. When we detected a significant interaction, we performed comparisons between each pair of restoration treatments using Tukey's method. As in the plant quality analysis, we used Wald type II chi-square tests to evaluate the influence of the fixed-effects adult morphological traits. We calculated the fixed-effects parameter estimates using the `effects` function in the `effects` package (Fox 2003) in R. Finally, we compared the variance in forewing length between restoration treatments using an F test.

To assess the effect of tree removal, damming, and their interaction on the allometric relationship between forewing length and body mass, we again used linear mixed models fit by restricted maximum likelihood. Forewing length and body mass were natural log-transformed prior to analysis. These transformations both normalized the variables (in the case of body mass) and allowed for the estimation of the slope and intercept for the best-fit lines describing each allometric relationship. As in the models evaluating restoration's effect on morphological traits alone, we analyzed restoration's effect on allometry separately by sex. Each model included the fixed effects of tree removal, damming, body mass, their interactions, and the nested random effects

of cage within plot within block. We performed Wald type II chi-square tests for the influence of the fixed effects; a significant interaction between restoration treatment and body mass would indicate that the regression lines have different slopes and thus that the allometric relationship differs between treatments.

Dispersal

To relate adult morphological traits to butterfly dispersal, we performed a capture–mark–recapture study from 21 May to 19 June 2013 in two experimental blocks. Each plot ($n = 8$) was surveyed daily for 20 min, during which time we attempted to capture all Appalachian brown butterflies observed. When we captured an unmarked butterfly, we marked it on the underside of its wing with a unique numeric code and placed it in a glassine envelope for transport to a central location for measurement where we weighed and measured its forewing length. We then returned newly marked individuals to their original plot and released them at a fixed location near the center of the plot. For recaptured butterflies, we recorded their codes and recapture locations before releasing them where they were recaptured.

We analyzed capture–mark–recapture data using multistate models within the program MARK (White and Burnham 1999). Different states represented different plots where a butterfly could be captured or recaptured, and transition rates among states represented dispersal probabilities between pairs of plots. We fit 98 models (Appendix S1) varying in their assumptions about the determinants of adult survival, detection probability, and dispersal among plots. Survival was modeled as a function of sex and

restoration treatment in the plot where the butterfly was found. Detection probability was modeled as a function of tree removal. Emigration rates were modeled as a function of sex, forewing length, body mass, the ratio of forewing length to body mass, and restoration treatment of the plot from which a butterfly originated. Because butterflies tend to fly along stream corridors, we evaluated models in which distance between plots was measured as Euclidean distance and as stream distance. Models were ranked using Akaike's information criterion (AIC) and the 95% confidence interval (CI) for parameter estimates for all models with AIC_c scores within two of the top model (Hurvich and Tsai 1989). Predictors whose coefficients had 95% CIs that did not overlap zero were determined to have statistically significant effects.

RESULTS

Plant quality

Tree removal had strong effects on the chemical composition and physical properties of *C. mitchelliana* leaves (Table 1), and considering how these traits related to herbivore performance, some improved and some deteriorated in response to restoration. Leaves from tree removal plots had a significantly lower percentage of N ($\chi^2_1 = 29.99$, $P < 0.0001$), which resulted in a significantly higher C:N ratio ($\chi^2_1 = 30.94$, $P \leq 0.0001$). The effect of tree removal on percentage of C varied by month (Appendix S2: Table S1, $\chi^2_1 = 10.71$, $P = 0.0010$). Furthermore, leaves in tree removal plots were significantly tougher than those in shaded plots ($\chi^2_1 = 17.45$, $P < 0.0001$). Leaves from tree removal plots also had higher leaf dry matter content ($\chi^2_1 = 46.70$, $P < 0.0001$), and specific

Table 1. Mean \pm SE of plant quality traits in plots with trees ("control;" includes both control and streams dammed only plots) and with >90% trees removed ("tree removal;" includes both trees removed only and trees removed and streams dammed plots).

Restoration treatment	Percentage of nitrogen		Carbon:nitrogen		Percentage of silica [†]		Leaf dry matter content		Leaf toughness [‡] (g)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Tree removal	1.53	0.02	34.39	0.56	0.01	0.00	0.38	0.00	615.30	15.66
Control	1.82	0.03	28.07	0.45	0.02	0.00	0.33	0.00	485.77	13.54

Note: All of the listed traits were significantly different between treatments ($P < 0.05$).

[†] Only tested in May and August.

[‡] Not measured in October.

leaf area varied by month (Appendix S2: Table S1, $\chi^2_1 = 6.08$, $P = 0.014$). At the same time, leaves from tree removal plots had lower percentage of Si ($\chi^2_1 = 64.51$, $P < 0.0001$). Neither damming nor the interaction between tree removal and damming affected the chemical composition or physical characteristics of *C. mitchelliana* leaves that we measured (Appendix S2: Table S2).

Adult traits

The total number of oocytes present in the ovaries of newly emerged, unmated females increased with body mass ($z = 2.85$, $P = 0.0044$), but restoration treatment did not affect the rate at which the total number of oocytes increased with increasing body mass ($\chi^2_1 = 2.31$, $P = 0.5102$) or the total number of oocytes ($\chi^2_1 = 1.26$, $P = 0.7396$; Appendix S2: Table S3). However, females emerging from plots with trees removed had a lower number of mature oocytes ($z = 2.32$, $P = 0.0200$; Fig. 1). Thus, while we observed mixed effects of restoration on plant quality traits related to herbivore performance, the lower number of mature oocytes in females from these

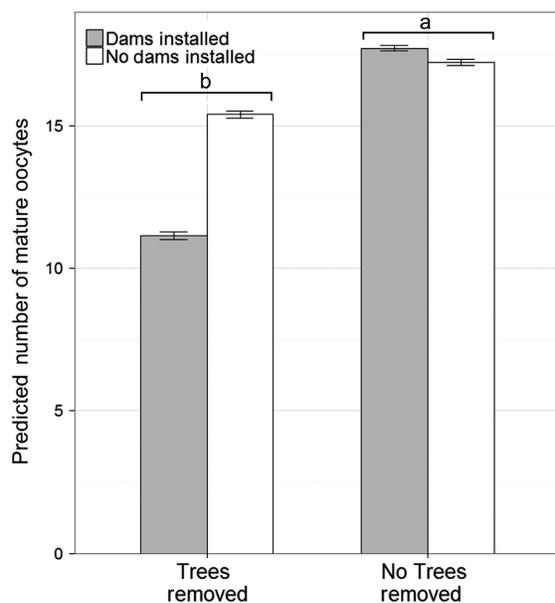


Fig. 1. Average number of mature (>3.5 OM) oocytes per female \pm SE as predicted by the generalized linear mixed model that takes into account female body mass. Females from plots with trees removed had significantly fewer mature oocytes ($z = 2.32$, $P = 0.02$), as indicated by different letters.

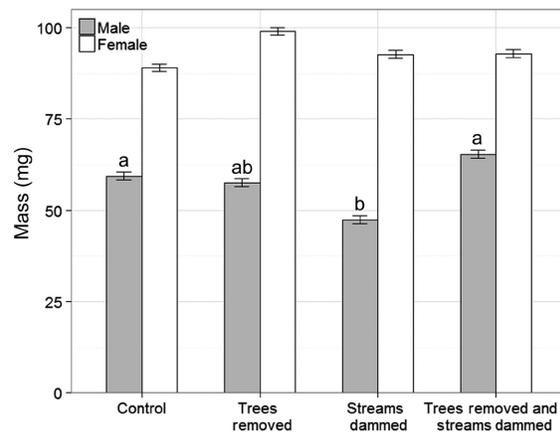


Fig. 2. Mean mass (mg) \pm SE for males and females across restoration treatments. Different letters represent significant differences between groups as determined by a Tukey's test ($P < 0.05$).

sites could indicate that tree removal has an overall negative effect on Appalachian brown fecundity.

Males from plots with both tree removal and damming ($z = -3.17$, $P = 0.0080$), as well as males from control plots ($z = -2.69$, $P = 0.0354$), were significantly heavier than males from plots that had only been dammed (Fig. 2). Male forewing length did not differ between restoration treatments ($\chi^2_1 = 0.18$, $P = 0.6687$; Appendix S2: Table S3). Neither female body mass ($\chi^2_1 = 0.58$, $P = 0.4477$) nor forewing length ($\chi^2_1 = 0.01$, $P = 0.9272$) differed by restoration treatment (Appendix S2: Table S3), but forewing length was significantly more variable for females emerging from dammed plots compared to plots that had not been dammed (0.005 vs. 0.002; $F_{1,52} = 2.60$, $P = 0.008$).

The slope of the allometric relationship between forewing length and body mass was significantly steeper for females from dammed plots compared to those from plots without dams ($\chi^2_1 = 10.09$, $P = 0.0015$; Fig. 3A). The shallower slope for females from plots without dams indicates that as body mass is reduced, a relatively larger forewing length is exhibited. As forewing length is correlated with wing area, smaller females from plots without dams have a lower wing loading ratio (body mass/wing area) compared to small females from dammed plots. Male allometric relationship was not affected by restoration treatment ($\chi^2_1 = 0.37$, $P = 0.5457$).

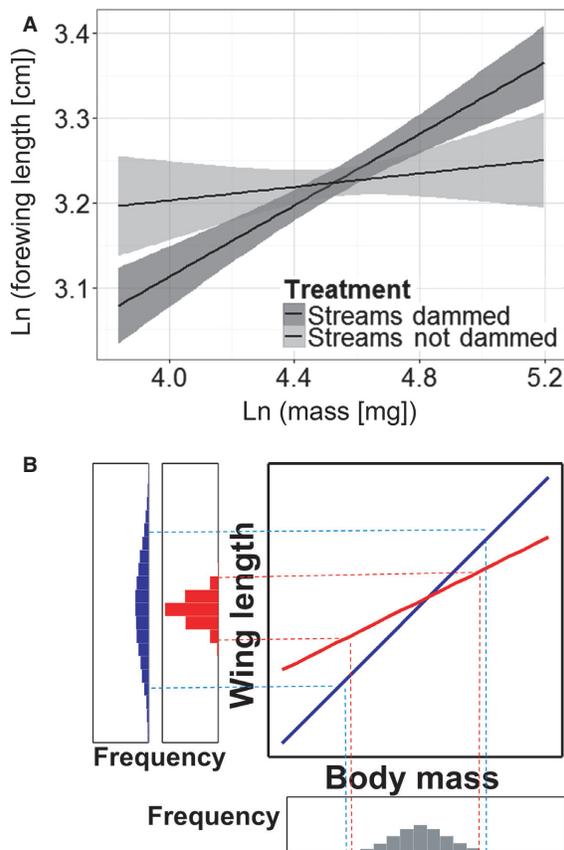


Fig. 3. Effects of changes in body mass and allometry on forewing length. (A) Allometric relationship between body mass and forewing length for females emerging from dammed vs. not dammed plots. The best-fit allometric equation for females from dammed plots was \ln forewing length = $2.27 + 0.21 \times \ln$ body mass, $r^2 = 0.70$. For females from plots without dams: \ln forewing length = $3.04 + 0.04 \times \ln$ body mass $r^2 = 0.04$. (B) Potential effect of a change in allometry on the variance in forewing length among individual butterflies. Even if restoration does not change the distribution of body mass among individuals (gray histogram below), a change in allometry from the red line to the blue line would lead to greater variance in forewing length among individuals (compare the red and blue histograms at left).

Dispersal

In total, we marked 56 butterflies, of which we recaptured 31 butterflies at least once. The top statistical model describing butterfly dispersal included sex, with males more likely to disperse, an effect of restoration treatment, with butterflies

less likely to emigrate from dammed than from undammed plots, a positive effect of butterfly body mass on emigration rate, and a negative effect of distance on immigration rate. The second best model included a negative effect of forewing length-to-body mass ratio on dispersal rates, which was likely caused by the positive effect of body mass on dispersal rates. In the top two models, the effect of butterfly body mass on dispersal was statistically significant (i.e., the 95% confidence interval of the parameter estimates does not overlap 0). There was virtually no difference in AIC_c weight between the top two models, and very little between the top three (Table 2). Thus, while there is support for a positive effect of butterfly mass on dispersal, including mass as a covariate did not add much explanatory power to our analysis.

DISCUSSION

Tree removal and stream damming were successful restoration treatments by traditional measures: The butterflies' host plant abundance increased and individuals released into plots persisted (Aschehoug et al. 2015). But for restoration to be successful over a longer time frame and larger spatial scale, other aspects of habitat quality and their influence on focal taxa are also important.

While the abundance of sedges tripled in tree removal plots (Aschehoug et al. 2015), we found that tree removal altered leaf traits in ways that are consistent with reduced host plant quality. Poor host quality could translate into fewer larval nutrients available for initial reproductive investment, as represented by the number of oocytes that a female has ready to lay relative to her total lifetime potential fecundity (Jervis et al. 2005), with potential negative implications for demography. Boggs (1986) found that for moths that do not feed at all as adults (as is the case here), oviposition rate declines dramatically with age. This suggests that a reduction in initial reproductive effort may result in reduced lifetime reproductive success. Our finding that females from plots with trees removed (regardless of stream damming) had significantly fewer mature oocytes in their ovaries upon adult emergence (Fig. 1) supports the hypothesis that tree removal reduced the host plant quality of *C. mitchelliana* for

Appalachian brown caterpillars. That forewing length and body mass did not differ between restoration treatments (Fig. 2; Appendix S2: Table S3), however, suggests that females devoted their limited larval resources toward conserving morphological characteristics at the expense of developing mature oocytes. This represents a trade-off between initial reproductive investment and dispersal that is supported in Lepidoptera at both the intra- (Hanski et al. 2004) and interspecific levels (Jervis et al. 2005).

While stream damming did not alter the physical or chemical properties of leaves (Appendix S2: Table S2), it did alter the body plan of females (Fig. 3A) and decreased the likelihood of adult emigration (Table 2). Damming altered the allometric relationship between body mass and forewing length for female butterflies, such that forewing length increased more steeply with body mass for females from dammed plots, without altering female body mass. Instead, females emerging from dammed sites demonstrated an increase in forewing length variance, resulting in a higher fraction of individuals with long wings but also an increase in the fraction with short wings (compare the red and blue histograms in Fig. 3B). Increased intraspecific variation in morphology has been demonstrated both theoretically and empirically to affect dispersal (Brown and Crone 2016 and references therein). Small females from dammed sites, with short wings, would have a higher wing loading ratio compared to small females from plots without dams, making dispersal relatively more energetically costly, discouraging dispersal. Conversely, small

females from plots without dams demonstrated body plans more favorable for dispersal, which may be an adaptive response to facilitate escape from poor quality habitats. This idea is supported by our top model describing Appalachian brown dispersal, where damming reduced emigration of adults (Table 2).

At the same time, the steeper allometric relationship for butterflies from dammed sites suggests that heavy females from these sites also had relatively longer wings, likely promoting dispersal. Our finding that damming reduced emigration of adults from plots suggests that for Appalachian browns, the increase in females with short wings and high wing loading ratios outweighs any effect of flooding to increase dispersal capacity by elevating the number of adults with long wings and low wing loading ratios. It may also be the case that, because damming did not alter male allometry and males dispersed more than females (Table 2), effects of damming on male dispersal overwhelmed any effects of changing allometry on female dispersal.

While tree removal resulted in host plants with tougher leaves and lower N content, tree removal likely increased plant quality in other ways, possibly promoting restoration success. In particular, tree removal halved the percentage of Si in leaves (Table 1). As Si plays a role in antiherbivore defense, with negative effects on insects (reviewed by Reynolds et al. 2009) and small mammals (Wieczorek et al. 2015), a reduction in the percentage of Si would likely improve herbivore demography. Males from plots with trees removed and damming were heavier compared to males from

Table 2. Top statistical models describing butterfly dispersal likelihood from MARK analysis.

Variables in model†	Delta AIC _c	AIC _c weights	Number of parameters	Deviance	Mass effect‡	Length effect‡	Length:mass effect‡
Sex dam mass	0	0.25	9	758.5	+		
Sex dam length:mass	0.3	0.22	9	758.7			-
Sex dam	0.4	0.2	8	761.1			
Sex dam mass length:mass	2.2	0.08	10	758.4	0		0
Sex dam length mass	2.2	0.08	10	758.4	+	0	
Sex dam length	2.5	0.07	9	761		0	
Sex dam length length:mass	2.5	0.07	10	758.7		0	-

Note: AIC, Akaike's information criterion.

† All models included a negative effect of distance between sites and estimated greater dispersal rates for males than for females. When included, damming always had a negative effect on emigration rates.

‡ Estimated effects for which the 95% confidence intervals do not span 0 are indicated by a "+" or "-"; estimated effects with 95% confidence intervals spanning 0 are indicated by "0".

sites that had only been dammed (Fig. 2). Given that our top model describing Appalachian brown dispersal included a positive effect of body mass on emigration rate (Table 2), tree removal likely promoted male dispersal. As the maintenance of dispersal is a key restoration strategy to enhance population viability (McAlpine et al. 2016), tree removal could promote restoration success. Our results highlight that restoration's effects on plant traits can translate into opposing effects on host plant quality for target herbivores.

Our knowledge regarding restoration's complex effects on host plant quality and butterfly traits can inform management decisions. We frame this discussion around St. Francis' satyr, the federally endangered butterfly motivating our restoration experiment, recognizing that our results for Appalachian brown butterflies may not generalize. Our results suggest that different habitat restoration strategies may be required, depending on whether managers prioritize population growth rates or metapopulation connectivity. If a restoration effort's primary goal is to increase metapopulation connectivity, tree removal combined with stream damming would be an appropriate form of habitat restoration as these sites promote dispersal for males via an increase in body mass. On the other hand, if population growth within a restored site is prioritized, stream damming alone would be an appropriate management technique. Stream damming does not reduce plant quality as tree removal does (although leaves from plots with dams did have increased Si), and butterflies were less likely to emigrate from these sites. Restoration of a network of patches modified with stream damming would therefore be more likely to require seeding of new sites with St. Francis' satyr to establish new populations. Additionally, the increased variation in forewing lengths among females from plots with stream damming could influence the population's critical minimum patch size (Brown and Crone 2016). As an alternative, restoration areas could themselves include spatially aggregated variation in tree removal and damming.

While we have attempted to connect variation in habitat quality to butterfly dispersal, the ability to generalize these interpretations must be tested. In particular, dispersal was measured in a separate study and used individuals whose natal location was unknown. For instance, an

individual that we first captured in a plot with stream damming may have spent its larval development in a tree removal plot and immigrated to the dammed plot prior to observation. Additionally, host plant density, which increased in tree removal sites but did not increase in sites with dams (Aschehoug et al. 2015), likely has a greater effect on adult movement than host plant quality. Future work involving rearing caterpillars on fixed quantities of host plants that vary in quality, measuring the morphological traits from the resulting butterflies, and quantifying these individuals' dispersal in flight mills would strengthen the connection between host plant quality, adult morphological traits, and dispersal.

In summary, we demonstrate that restoration, potentially through its effects on plant quality, caused complex changes in adult morphology and fecundity. Our research also suggests that these morphological changes affect the dispersal of our focal species. As enhancing population viability and metapopulation connectivity are key elements to restoration strategies of vulnerable animal taxa, our results highlight the need to consider restoration's effects on host plant quality, and on habitat quality more broadly, when predicting the impacts of such actions on the recovery of target herbivores.

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